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Bulletin of the British Museum (Natural History)

Foraminifera of the Togopi Formation, eastern Sabah, Malaysia

J. E. Whittaker & R. L. Hodgkinson

Geology series Vol 31 No 1 29 March 1979

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Foraminifera of the Togopi Formation, eastern Sabah, Malaysia

J. E. Whittaker and R. L. Hodgkinson

Department of Palaeontology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

One hundred and twenty-five species are described and figured from a section in the upper Togopi River, type-locality of the Togopi Formation, eastern Sabah, Malaysia. Eighty-six per cent of the fauna is living today in the area. The following seven species and one variety are new: *Ammonia togopiensis*, *Bolivina sabahensis*, *Cellanthus biperforatus*, *C. hailei*, *Cribroelphidium dentense*, *Peneroplis planatus* var. *annulata*, *Pseudomassilina medioelata* and *Textilina subrectangularis*. *Florilus asanoi* is proposed as a new name for *Nonion japonicum* Asano, 1938.

The age of the Togopi Formation is reassessed on the basis of benthic foraminifera and is considered to be mainly of Pliocene age.

Introduction

The Togopi Formation, the uppermost sequence of mainly marine clays making up the Dent Group, is named after the Togopi River, eastern Sabah, Malaysia. The name was first published by Reinhard & Wenk (1951) but it had previously been used in a Sabah Shell Petroleum Company's (SSPC) internal report as early as 1938. Dr E. Wenk himself made the first collection of fossils (Mollusca) in 1937, some of which were described by Cox (1948). A further collection of macrofossils was made by P. Collenette in 1950, the Mollusca being listed by Nuttall (1960). Cox dated Wenk's material, which was dominated by gastropods, as Pliocene or possibly U. Miocene, while Nuttall considered Collenette's samples to be almost certainly Pleistocene. The former collection came from the Togopi River, but there is some confusion as to the exact provenance of Collenette's (Nuttall 1965).

In 1961 Dr N. S. Haile collected 18 samples from the type area for the Togopi Formation from its supposed boundary with the underlying Ganduman Formation to where it disappears under the coastal alluvia (for details see Haile & Wong 1965). From these Nuttall (1965) listed almost 200 species of Mollusca and after a detailed examination of the fauna assigned a Plio-Pleistocene age, equivalent to the Bantamian–Sondian stages of Java, to the Togopi Formation. Haile & Wong (1965 : 83) list identifications of teleostan otoliths by F. Stinton (Stinton 1963) and echinoderms by R. P. S. Jefferies together with a small foraminiferal fauna, identified by SSPC palaeontologists. The foraminifera came from samples collected by Wenk and Parsons between 4 and 13 km west and north-west of Dent Haven, but only a few genera and species were recognized.

Eleven of Haile's original samples were available for micropalaeontological examination, and in view of the richness of the fauna (125 species) it was decided to describe it fully and to attempt an age determination using the smaller benthic foraminifera. Planktonic foraminifera are unfortunately few in the Togopi Formation. Since 86% of the fauna still lives in the Indo-Pacific today it has also been possible to correct some common misidentifications of Recent species by referring back to the original collections of Brady, Parker & Jones, Carpenter, Williamson and Heron-Allen & Earland which are preserved in the BM(NH). A number of benthic species are now thought to be extinct and these are listed as of possible biostratigraphic use in the future.

Four samples from the small Wenk and Collenette collections have been examined for foraminifera but yielded no additional species. They are not dealt with any further in this paper.

The stratigraphy of the Dent Group is first discussed. The ages of the Sebahat and Ganduman Formations given by Haile & Wong (1965) are revised and the foraminiferal faunas reinterpreted in the light of recent advances in Tertiary biostratigraphy. A description of the Togopi stratigraphy and the material from the type-area which forms the basis of this work is then covered in detail. The occurrence of the foraminifera is summarized, their palaeoecology considered, and finally the overall evidence of the age of the Togopi Formation is presented.

The planktonic foraminifera have been identified and photographed by Mr H. A. Buckley, Department of Mineralogy, British Museum (Natural History).

Acknowledgements

We are indebted to our colleague Dr C. G. Adams for his encouragement and guidance in the preparation of this work and for his careful reading of the manuscript. To Dr D. J. Belford (Bureau of Mineral Resources, Canberra) goes our thanks for valuable discussions and for comparing a number of our species with his own from the Neogene of Papua–New Guinea; Dr R. W. Ponder (James Cook University, Townsville) also contributed a lively correspondence on several problematic species. Dr P. Marshall (formerly of University College, London) provided us with topotypic material of some of d'Orbigny's Caribbean species, while Dr H. Billman (formerly of the Union Oil Company) is also thanked for his kindness in making available to us examples of index and important marker fossils from the Kutei Basin, Indonesia. Dr R. Cifelli (Smithsonian Institution) readily arranged several loans of type-specimens. Dr J. R. Haynes (University College of Wales, Aberystwyth) gave us many helpful suggestions on taxonomic matters, while our colleague Mr C. P. Nuttall provided valuable information on the Togopi samples and their molluscan faunas.

The photography was undertaken by the senior author and by members of the Department of Central Services, British Museum (Natural History); to the latter we are especially indebted for their careful work. Some technical assistance was provided by Miss C. A. Harrison and, in the early stages, by Mr D. I. Dixon, formerly of the Museum's staff. Mrs E. M. Richards typed the manuscript.

Methods

The dry clay samples were disaggregated by boiling in a weak solution of hydrogen peroxide. The sediment was then washed through a series of sieves, the finest being 200 mesh (aperture: 75 microns), and dried. The original weight of the samples is not known, having first been examined for mollusca; however, the amount of material processed in the present study varied between 200 and 700 gm, five of the samples weighing approximately 400 gm. In order to speed up the examination process, the residue, obviously variable depending on the size of the clay fraction, was halved or quartered, and half (or a quarter) subjected to carbon tetrachloride flotation. Where the residue was large the flotation process was repeated and in the coarsest grade, when large specimens were present, bromoform was used. As no statistical study was to be attempted, only the floated portion and its residue were examined.

The friable limestones (NB 9446, NB 9448) and part of the sandstone (NB 9453) were either crushed and washed, or sectioned.

Internal structures of the foraminifera were examined: (a) by vertical, horizontal and oblique thin- and block-sectioning using a 'Lakeside 70' cement mount; (b) by immersion in various clearing fluids (usually clove oil); (c) by solution with a weak hydrochloric acid and 'Cellofas' 'mush', the specimen first being mounted in 'Lakeside'; and (d) by 'heat splitting' to produce half-sections of the Nummulitidae.

Most of the species have been illustrated using a Cambridge Mk II 'Stereoscan' scanning electron microscope, the micrographs having been taken mainly by one of the authors (J. E. W.). The specimens to be photographed were first cleaned with a 25% solution of the enzyme cleaning agent 'Decon' and placed on aluminium stubs. A variety of stub mounting techniques were used. In some cases a glass cover-slip was cemented on to the stub using silver 'dag' and the foraminifera were then mounted on the glass using 'Cellofas'; in other cases the specimens were directly mounted on the stub using 'Kodaflat' adhesive. A third technique, of mounting on a piece of negative film which had previously been cemented to the stub with 'Durafix', also proved satisfactory; the gelatine of the film when wetted provides enough adhesive to anchor the smaller foraminifera sufficiently. The specimens were then coated with several layers of gold before scanning and photography.

Part of Pl. 8, the whole of Pl. 9 and the thin sections of Pl. 10 were photographed with a Watson 'Holophot' Photomicroscope by the Museum's photographic unit.

The text-figures were mainly drawn by one of us (R. L. H.) with the aid of a light microscope and camera lucida attachment. The measurements of *Operculina/Nummulites* were taken from tracings of the embryonic apparatus on the Projectina (Model 4014) microscope.

Biostratigraphy

Stratigraphy of the Dent Group

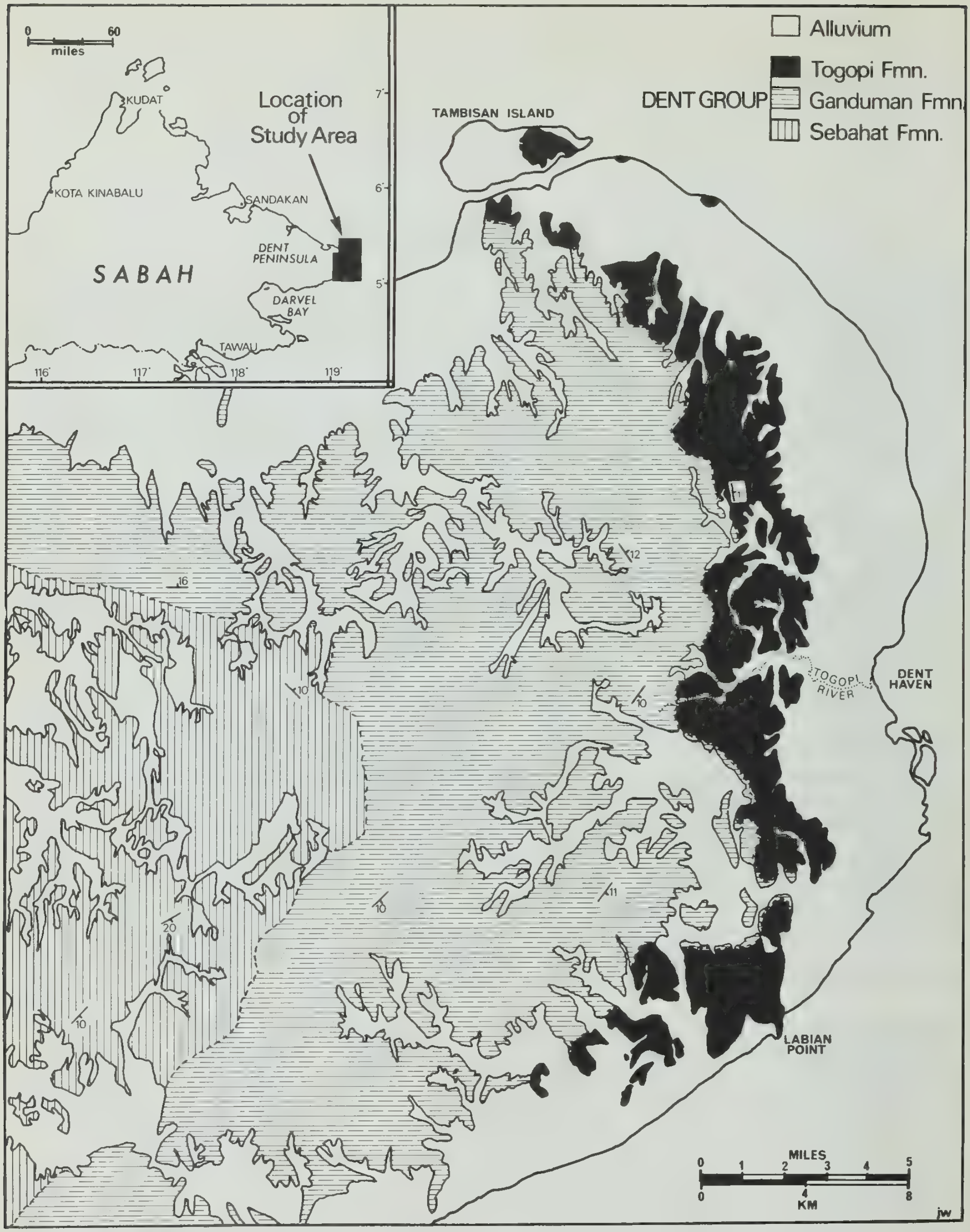
The Dent Group of the eastern Dent Peninsula, Sabah, comprises, in ascending order, the Sebahat, Ganduman and Togopi Formations. A thick (*c.* 14 000 ft or 4300 m) mainly marine sequence of predominantly clastic sediments with subordinate limestones, it locally overlies the Miocene Segama Group unconformably. The Togopi Formation is itself overlain with slight unconformity by about 100 ft (30 m) of Quaternary terrace and Recent river alluvium (Figs 1, 2). The main structural feature is a broad anticlinal uplift trending ENE down the centre of the peninsula, off which the three formations dip gently in a more or less conformable sequence.

Sebahat Formation. This is estimated by Haile & Wong (1965 : 74) to be over 7500 ft (2290 m) thick and was laid down in the sublittoral and neritic zones of the Neogene sea. They also state (1965 : 75) that it contains abundant foraminifera which have been identified by SSPC micropalaeontologists; these include rich planktonic faunas, larger foraminifera and small benthics, none of which has ever been described or illustrated. This Formation was dated as 'late Tf (late Miocene) to early Tg (early Pliocene)' by Haile & Wong. *Globigerinoides obliquus* Bolli is said to characterize the greater part of the unit. This, according to Postuma (1971), ranges up to Zone N18 (Upper Miocene/Pliocene boundary), but Blow (1969) would extend the range as far as Zone N22 (Pleistocene). In the lower part of the Formation several good age indicators are however present: *Globorotalia mayeri* Cushman & Ellisor, *Globigerinoides subquadratus* Brönnimann, *Globorotalia praemenardii* Cushman & Stainforth and *G. fohsi* forma *robusta* Bolli. Their joint occurrence suggests an age not older than Zone N12 or younger than the early part of Zone N13 (M. Miocene). The Tabin Limestone Member (middle Sebahat Formation) is said by Haile & Wong to contain *Cycloclypeus* (*Katacycloclypeus*), a larger foraminifer believed to be restricted to Lower Tf (M. Miocene) (*fide* Adams 1970). This identification has recently been confirmed by Dr Adams (personal communication), who has examined four samples of limestone from a 30 ft (9 m) bed west of the Tabin River. Apart from *C.* (*K.*) *annulatus* Martin, other age-diagnostic forms such as *Orbulina* sp. (Tf/N9–Recent) and *Lepidocyclina* (*Nephrolepidina*) sp. (Td–Upper Tf) are present. Thus the Sebahat Formation is probably Middle to Upper Miocene (Lower–Upper Tf of Adams 1970) in age.

Ganduman Formation. This is poorly fossiliferous. It is some 5000 ft (1500 m) thick, and an abundance of lignite and plant remains suggests a period of shallowing and very rapid deposition close to a large river mouth with extensive coastal swamps and mangroves, very similar in fact to the coastal environment of the Dent Peninsula today. A few specimens of *Globigerinoides obliquus* Bolli have been found in the lower part of the formation, but they could have been reworked from the Sebahat Formation. The Ganduman is probably late Miocene or early Pliocene in age.

Togopi Formation. This marks a return to shallow marine sedimentation (inner shelf to littoral). It is the youngest unit of the Dent Group and crops out in a curved belt, 2–3 miles (about 4 km) wide, extending from Tambisan Island in the north to the Merah River in the south (Fig. 1). The type locality and section is in the upper reaches of the Togopi River; few exposures are known elsewhere. Dips are low, usually under 10°, towards the north-east, east and south-east around the nose of the Sebahat anticline.

In the river section the boundary with the underlying Ganduman Formation is said to be a rather sharp lithological change from grey sand with pebbly beds up to 1 in (25 mm) thick,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KUDAT
Location of Study Area
KOTA KINABALU
SANDAKAN
DENT PENINSULA
SABAH
DARVEL BAY
TAWAU
116°
117°
118°
119°
7°
6°
5°
Alluvium
Togopi Fmn.
DENT GROUP
Ganduman Fmn.
Sebahat Fmn.
TAMBISAN ISLAND
12
16
10
10
TOGOPI RIVER
DENT HAVEN
11
10
20
10
LABIAN POINT
MILES
0 1 2 3 4 5
0 4 8
KM
jw

Fig. 1 The stratigraphy of the eastern part of the Dent Peninsula, Sabah (after Haile & Wong 1965).

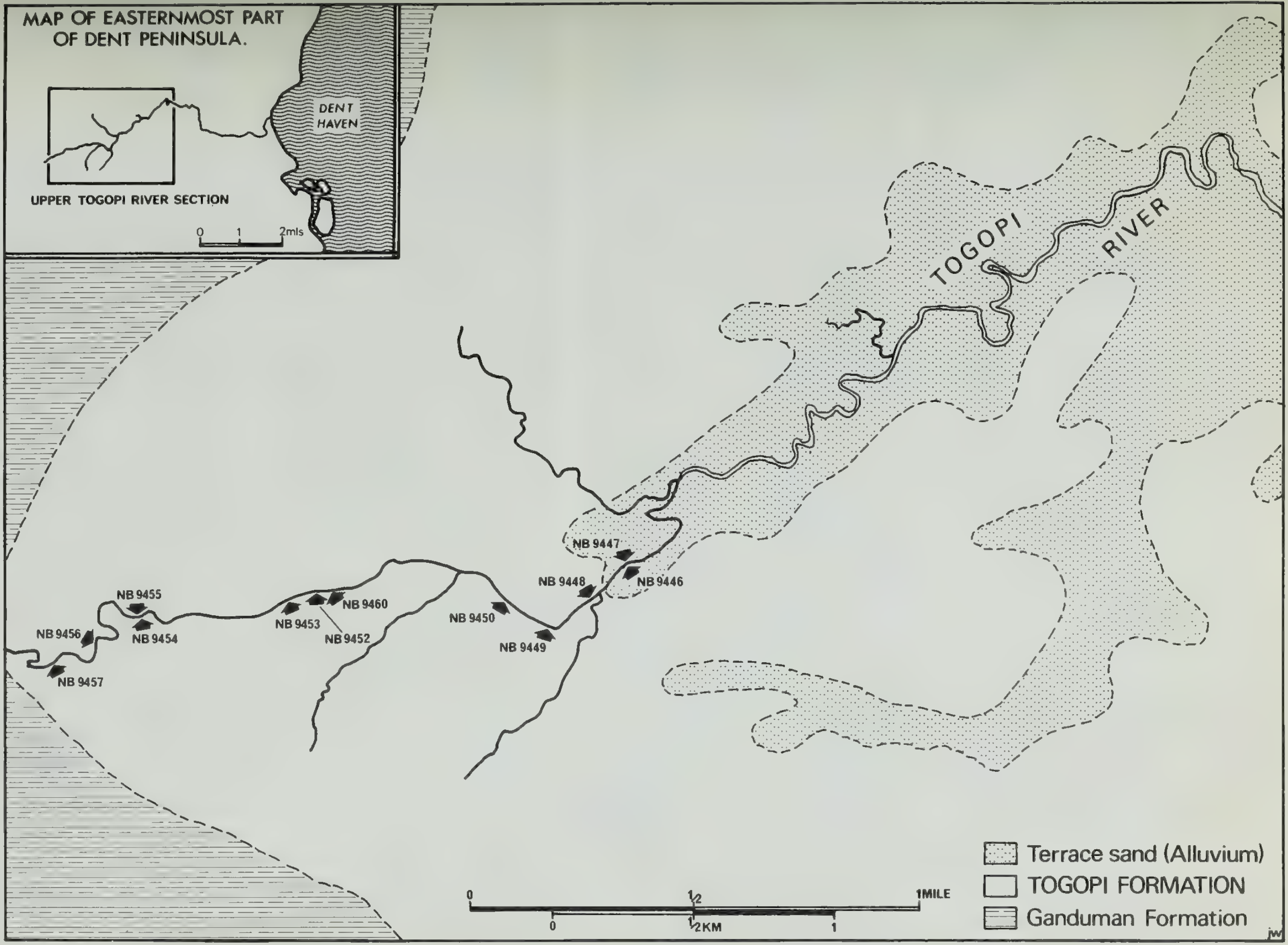
MAP OF EASTERNMOST PART OF DENT PENINSULA.
DENT HAVEN
UPPER TOGOPI RIVER SECTION
0
1
2mls
TOGOPI
RIVER
NB 9447
NB 9446
NB 9448
NB 9449
NB 9450
NB 9460
NB 9453
NB 9452
NB 9455
NB 9454
NB 9456
NB 9457
0
½
1MILE
0
½KM
1
Terrace sand (Alluvium)
TOGOPI FORMATION
Ganduman Formation
jw

Fig. 2 Map of the upper Togopi River Section, eastern Dent Peninsula, Sabah, showing the location of samples (after Nuttall 1965).

cemented with limonite and full of plant and wood fragments, to the characteristic olive-grey and bluish-grey poorly-bedded clays of the lower Togopi (Haile sample NB 9456/7) in which plant remains are rare according to Haile & Wong (1965 : 82). No unconformity has been reported.

Samples NB 9450 up to and including NB 9456/7 were collected from grey to blue-grey sandy clays cropping out in the river banks (Fig. 2). In the area from which NB 9453 was collected there are irregular concretionary beds of fossiliferous grey calcareous sandstone. At an 8 ft (2·4 m) exposure from which NB 9449 was taken the lithology had changed slightly to a blue-grey plastic clay and at NB 9448 a brownish limestone with some 9 in (230 mm) nodules of harder ferruginous limestone was exposed for a thickness of 10 ft (3 m), the whole being covered by a tufa crust. The topmost samples are blue calcareous clays set amongst rubbly limestone rich in corals and reefal debris, the sequence thereafter disappearing under Quaternary alluvium. Assuming an average dip of 5°–10° towards the east and south-east, the type-section must approach 700 ft (210 m) in thickness. The formation is said to attain a maximum thickness of *c.* 1350 ft (410 m) in the south of the area (Haile & Wong 1965 : 81).

Elsewhere, the only other sections studied were by Clements (of SSPC), the results being summarized by Haile & Wong (1965). He had two rentis lines (jungle trails) cut to the north and south of the Togopi River. Along the northern line, the basal beds were reported to be almost undistinguishable from the Ganduman Formation but photogeological evidence suggested an angular unconformity. In the southern cut Clements found a basal conglomeratic sandstone suggesting that the lower boundary of the Togopi represents a shallow marine transgression and is probably slightly unconformable.

Distribution and palaeoecology of the Togopi Foraminifera

Eleven of the best samples collected by Dr N. S. Haile from the Togopi River section were selected for study. A description of these samples, in ascending order of the succession, and their foraminiferal faunas, together with a palaeoecological interpretation, are outlined below. A distribution chart is provided (Table 1, pp. 12–13).

The basal samples, NB 9456 and NB 9457, became mixed in transit and have, therefore, been treated together. Six species were found, of which only *Pseudorotalia catilliformis* (Thalmann) and *Cellanthus biperforatus* sp. nov. are common. Sample NB 9455 (see Fig. 2) contains only two species, *P. catilliformis* being dominant. The foraminifera for the most part are badly abraded and corroded, and support Nuttall's (1965) conclusion that the lowermost Togopi was laid down in very shallow, muddy, turbulent, and possibly brackish water close to shore. Alternatively, the microfauna could have been washed in from the sublittoral zone.

Sample NB 9454 contains the first really large fauna. Some 25 species are present, all indicative of shallow inner-shelf conditions. Ten species of the Miliolidae occur (see Table 1), though none of them are common, together with five species of the Elphidiidae, the first species of *Lagena* and *Operculina ammonoides* (Schröter). By far the largest elements in this fauna, however, are the larger rotaliids, *Pseudorotalia catilliformis* (Thalmann) still remaining dominant. NB 9453 is a hard calcareous sandstone which has been disaggregated and also examined by means of thin sections. Although only 10 species have been identified with certainty it appears to contain a similar fauna to NB 9454. Samples NB 9460 and NB 9452 were from approximately the same horizon although the latter (see Fig. 2) was collected some distance to the west of NB 9460; their faunas, however, are quite different. NB 9460 yielded 27 species, dominated almost entirely by large members of the Rotaliidae (common *Asterorotalia pulchella* (d'Orbigny) and *Pseudorotalia* spp.) and members of the Elphidiidae; only one miliolid was found (*Quinqueloculina curta* Cushman), but the first planktonic foraminifera occur (see Table 1). Fifty-seven species have been recorded from NB 9452. Here the fauna is characterized by inner-shelf larger foraminifera which today live on stable substrates, often associated with sea-grass and marine algae down to a depth of about 30 m (usually, however, about 10 m). Our four main species of the Nummulitidae (*Nummulites* cf. *amplicuneatus* (Cole), *N. tamanensis* (Vaughan & Cole), *Operculina ammonoides* (Schröter) and *O. bartschi* Cushman) make up the bulk of the fauna together with very large numbers of *Alveolinella quoyi* (d'Orbigny) and a few representatives of *Amphistegina* and *Hetero-*

stegina (see Table 1). The largest diversity of the Elphidiidae (nine species) also occurs in this sample; there are also abundant specimens of *Florilus asanoi* nom. nov.

Samples NB 9450 and NB 9449 probably represent sediments from the deepest, most open water locally present in 'Togopi times', though it is doubtful if a depth of 30 m was ever exceeded (Nuttall 1965 : 163). Here the foraminiferal fauna attains its greatest diversity, 78 and 86 species respectively. The agglutinating element, never strong, reaches its acme, and the Bolivinitidae, usually signifying deeper-water conditions, make their only significant appearance. In NB 9449, moreover (see Table 1), the 11 species of *Lagena* found in the Togopi Formation occur together in large numbers, while both the Miliolidae and Rotaliidae attain their largest diversity, 24 and 28 species, respectively. The algal-dwelling *Calcarina hispida* Brady is a significant member of the fauna in NB 9450, while at NB 9449 many attached species such as *Cymbaloporetta* spp. may indicate the presence of seaweed, associated with patch reefs. NB 9448 is a badly leached sample containing few recognizable species.

The uppermost samples present in the Togopi River section may signify a return to shallower water with a build-up of coral reef-patches. A significant proportion of these samples is made up of broken coral (probably transported) and it may be doubted whether true coral reefs occurred in this area at the time. Nevertheless, the lack of planktonic foraminifera compared with Recent shallow-water samples taken in Darvel Bay (H. Buckley, BM(NH), personal communication) is puzzling unless one postulates either a barrier (? coral-reef) to the open sea and thus reduced circulation, or a much higher sedimentation rate than at present. Samples NB 9447 and NB 9446 have 40 and 11 species respectively. Their preservation and often delicate nature suggests that they are life assemblages (cf. the broken corals). Significantly, the large species of *Pseudorotalia*, *Ammonia annectens* (Parker & Jones), *Asterorotalia inspinosa* Huang, and the previously almost ubiquitous *Asterorotalia pulchella* (d'Orbigny) are absent and have been replaced by smaller rotaliids such as *Ammonia beccarii* (Linnaeus) var. *tepida* (Cushman), *A. takanabensis* (Ishizaki) and *Pararotalia* cf. *nipponica* (Asano) (see Table 1). The Elphidiidae remain common to the end of the section, in particular *Elphidiella indopacifica* Germeraad.

Age of the Togopi Formation

Planktonic foraminifera. Only very few, usually immature, individuals, belonging to six species, were found in samples NB 9460 to NB 9447. These are:

Species	Range (after Blow 1969)
Hastigerina siphonifera (d'Orbigny)	N12–N23
Globigerina bulloides d'Orbigny	N16–N23
Globigerina quinqueloba Natland	N17–N23 (after Parker 1967)
Globigerinoides ruber (d'Orbigny)	N16–N23
Globiginoides sacculifer (Brady)	N6–N23
Globigerinita glutinata (Egger)	N16–N23

The upper part of the Togopi Formation cannot, therefore, be older than late Miocene (Zones N16/17).

Benthic foraminifera. Our taxonomic study of the Togopi foraminifera has enabled us to search the literature and establish a tentative stratigraphical distribution for 119 benthic species. There are, of course, a number of difficulties in determining overall ranges, not least of which is the impossibility of verifying original age determinations where accepted age-diagnostic species are absent.

Fig. 3 shows the distribution of the 15 species, thought to be extinct,[1] which occur in the Togopi Formation. Some may ultimately prove to be of importance stratigraphically and are discussed below in conjunction with the work of Billman & Kartaadipura (1975). *Nummulites tamanensis* (Vaughan & Cole), characterized by its trabeculae-like structures, is very distinctive, but its only previous record is from the Miocene of Trinidad. *Nummulites* cf. *amplicuneatus* (Cole) resembles a number of Plio-Pleistocene species from Bikini Atoll (Cole 1954). *Amphistegina* cf. *wanneriana*

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[1] But see Postscript, p. 106.

Fischer, to which our poorly-preserved specimens are tentatively assigned, has been previously reported only from the Pliocene of Ceram and Soemba, Indonesia. However, *Brizalina amygdalaeformis* (Brady) *iokiensis* (Asano), *Asterorotalia inspinosa* Huang and *Cellanthus adelaidensis* (Howchin & Parr) occur in the Togopi with some frequency, have all been recorded more often by previous workers, and do not appear to have been found in post-Pliocene sediments. None are found in the uppermost samples (Fig. 3), thus suggesting that these beds may be of Lower Pleistocene age. Nevertheless, two important species, both ranging from Miocene to Plio-Pleistocene, namely *Pseudorotalia catilliformis* (Thalmann) and *Cribrononion tikutoensis* (Nakamura), are also absent from the upper Togopi. The distribution of all five species may, therefore, be facies-controlled. Finally, five new species are listed in Fig. 3.

SPECIES \ SAMPLE №	NB 9456/7	NB 9455	NB 9454	NB 9453	NB 9460	NB 9452	NB 9450	NB 9449	NB 9448	NB 9447	NB 9446
Nummulites cf. amplicuneatus[1]						■					
Nummulites tamanensis[1]						■					
Amphistegina cf. wanneriana[2]						■	■				
Asterorotalia inspinosa[2]					■	■	■	■			
Brizalina amygdalaeformis iokiensis[2]						■	■	■	■		
Cellanthus adelaidensis[2]					■	■	■	■			
Ammonia togopiensis sp. nov.[3]	■				■	■	■	■		■	■
Cribrononion tikutoensis[3]			■		■	■	■				
Pseudoeponides japonicus[3]								■	■	■	
Pseudorotalia catilliformis[3]	■	■	■	■	■	■	■ ■				
Bolivina sabahensis sp. nov.[4]							■			■	
Cellanthus biperforatus sp. nov.[4]	■		■		■	■				■	■
Cellanthus hailei sp. nov.[4]				■		■	■	■		■	
Cribroelphidium dentense sp. nov.[4]						■					
Textilina subrectangularis sp. nov.[4]			■			■	■	■			

Fig. 3 The distribution of extinct species of foraminifera within the Togopi Formation. Sample numbers are arranged in ascending stratigraphical order, left to right.
[1] Species previously not known in post-Miocene deposits.
[2] Species previously not known in post-Pliocene deposits.
[3] Species previously not known in post-Plio/Pleistocene deposits.
[4] Species known only from the Togopi Formation (presumed extinct).

In 1969, van der Vlerk & Bannink attempted to show that the genus *Operculina* could be used to determine the age of a deposit using an analogous biometric method to that previously employed with *Lepidocyclina*. The results obtained from testing their hypothesis with two species of *Operculina* from the Togopi Formation are given in detail on p. 90. Although van der Vlerk & Bannink used only *Operculina* for their study, we endeavoured to extend their method to species of *Operculinoides* (= *Nummulites*). *Operculina ammonoides* (Schröter) and *Nummulites* cf. *amplicuneatus* (Cole) both gave Upper Pliocene results, which may be good evidence that sample NB 9452, if not the whole of the Formation, is of that age; unfortunately *Operculina bartschi* Cushman and *Nummulites tamanensis* (Vaughan & Cole) gave early Miocene and late Eocene dates respectively. Other species from rocks of known age measured for comparative purposes also gave conflicting results (see p. 91 and Fig. 63).

Billman & Kartaadipura (1975) have published a zonation, based on benthonic foraminifera, for the Miocene to Recent sediments of the Kutei Basin, east Borneo. As this area is little more than 400 miles (650 km) to the south of the Togopi River and contains very similar shallow water deposits to the Dent Group, their paper is of great importance in the present context.

The Kutei Basin zonation is reproduced in Fig. 4. Billman & Kartaadipura define the upper limit of each zone by the local extinction levels of the zonal species. Their uppermost zone is defined by the range of *Calcarina* spp. above the extinction level of *Ammonia ikebei* (Inoue & Nakaseko). Other important markers are *Pseudorotalia conoides* (d'Orbigny) [= *P. schroeteriana* (Parker & Jones), see p. 78] and *Asterorotalia pulchella* (d'Orbigny). N22/23 planktonic foraminifera and NN19/21 (Pleistocene–Recent) nannoplankton were also found. In the Togopi Formation, *Calcarina hispida* Brady, *P. schroeteriana* and *A. pulchella* occur almost throughout the section, *A. pulchella* being ubiquitous except in the highest two samples.

Smaller Benthic Foram. Zone	Other Important Benthic Zonal Markers	Planktonic Foram. Zone (BLOW, 1969)	Calcareous Nannoplankton Zone	Age
CALCARINA	PSEUDOROTALIA CONOIDES ASTEROROTALIA PULCHELLA	N22/23	NN19/21	PLEISTOCENE – RECENT
AMMONIA IKEBEI		?	?	PLIO-PLEISTOCENE
ASANOINA	PSEUDOROTALIA INDOPACIFICA var. ELPHIDIUM SP. 14 SIGMOIDELLA SP. (lower part only)	?	?NN12/16	PLIOCENE
PSEUDOROTALIA CATILLIFORMIS		N15/17	NN11	LATE MIOCENE
AMMONIA YABEI — —?— —			NN9/11	
		N13/14	NN7/8	MIDDLE MIOCENE

Fig. 4 Correlation of Smaller Benthic Foraminifera Zones with Plankton Zones in the offshore Kutei Basin, Indonesian Borneo (based on Billman & Kartaadipura 1975).

The *Ammonia ikebei* Zone, which lacks age-diagnostic plankton, is assigned a Plio-Pleistocene age on its stratigraphic position. Its top is placed at the highest occurrence of *Ammonia ikebei* [*non A. ikebei* (Inoue & Nakaseko), = *A. togopiensis* sp. nov., see p. 71]. This species is found in both the highest and lowest samples of the Togopi River section (Fig. 3), but is not known to be living today.

Nannoplankton and planktonic foraminifera are also rare in the preceding *Asanoina* Zone, but evidence from wells farther to the south suggests a Pliocene age for this zone. We do not have an *Asanoina* species like that figured by Billman & Kartaadipura (pl. 1, fig. 3), but the other important zonal markers, *Pseudorotalia indopacifica* (Thalmann) var. [a trend to *P. alveiformis* (Thalmann) seen particularly in Togopi sample NB 9460, see Pl. 10, fig. 8] and *Elphidium* sp. 14 [= *Cellanthus adelaidensis* (Howchin & Parr), see p. 83] occur in the Togopi Formation. *C. adelaidensis* would seem to be a good marker for the Pliocene (see above and Fig. 3). *Sigmoidella* sp. [= *S. elegantissima* (Parker & Jones)] is used by Billman & Kartaadipura to subdivide this zone (Fig. 4), its highest occurrence being within the lower half. However, our survey shows that this species probably ranges from Miocene to Recent.

The *Pseudorotalia catilliformis* Zone spans the time occupied by the deposition of the sediments in which the Kutei oil and gas reservoirs are now found. These sediments are indicative of very shallow water, nannoplankton and pelagic foraminifera are rare, but deeper-water intercalations prove a late Miocene age. In the Togopi Formation, *P. catilliformis* occurs in samples NB 9456/7 to NB 9452 (? NB 9450), after which it disappears (see Fig. 3). This may indicate either a facies change or extinction as the species does not appear to be living today. We have found, however, that specimens provided by Billman from the *Asanoina* Zone and labelled *P. tikutoensis* (Nakamura) are synonymous with *P. catilliformis*. This species must, therefore, as at Togopi, occur in

Table 1 Distribution chart of the Foraminifera species within the Togopi River section. Samples ar

	NB 9456/7	NB 9455	NB 9454	NB 9453	NB 9460	NB 9452	NB 9450	NB 9449	NB 9448	NB 9447	NB 9446
Ammonia annectens (Parker & Jones)	●	—	●	—	●	●	●	●	●	—	—
Ammonia togopiensis sp. nov.	●	—	—	—	●	●	●	●	—	●	●
Asterorotalia pulchella (d'Orbigny)	●	●	●	●	●	●	●	●	●	—	—
Cellanthus biperforatus sp. nov.	●	—	●	—	●	●	—	—	—	—	—
Florilus asanoi nom. nov.	●	—	—	—	●	●	●	●	—	—	—
Pseudorotalia catilliformis (Thalmann)	●	●	●	●	●	●	●	○	—	—	—
Cellanthus craticulatus (Fichtel & Moll)	—	—	●	—	●	●	●	●	—	●	—
Clavulina pacifica Cushman	—	—	●	—	—	—	●	●	●	●	—
Cribrononion reticulosus (Cushman)	—	—	●	—	—	●	●	●	—	●	—
Cribrononion tikutoensis (Nakamura)	—	—	●	—	●	●	●	—	—	—	—
Elphidiella indopacifica Germeraad	—	—	●	—	●	●	●	—	—	●	●
Lagena perlucida (Montagu)	—	—	●	—	●	●	●	●	—	—	—
Lagena striata (d'Orbigny)	—	—	●	—	●	●	●	●	—	—	—
Operculina ammonoides (Schröter)	—	—	●	●	●	●	●	●	—	●	—
'*Pseudonodosaria*' *glans* (d'Orbigny)	—	—	●	—	●	—	●	●	—	—	—
Pseudorotalia schroeteriana (Parker & Jones)	—	—	●	—	●	●	●	●	●	—	●
Quinqueloculina contorta d'Orbigny	—	—	●	○	—	●	—	—	—	—	—
Quinqueloculina curta Cushman	—	—	●	○	●	●	○	●	—	—	—
Quinqueloculina parkeri (Brady)	—	—	●	—	—	●	●	●	—	●	—
Quinqueloculina philippinensis Cushman	—	—	●	—	—	●	●	●	—	—	—
Quinqueloculina polygona d'Orbigny	—	—	●	—	—	—	—	●	—	●	—
Quinqueloculina pseudoreticulata Parr	—	—	●	●	—	●	●	●	—	●	—
Quinqueloculina sulcata d'Orbigny	—	—	●	—	—	●	●	●	—	—	—
Textilina subrectangularis sp. nov.	—	—	●	—	—	●	●	●	—	—	—
Triloculina bradyana (Cushman)	—	—	●	○	—	●	—	●	—	—	—
Triloculina subgranulata Cushman	—	—	●	—	—	—	—	●	—	●	—
Triloculina trigonula (Lamarck)	—	—	●	—	—	●	—	●	●	●	—
Cellanthus hailei sp. nov.	—	—	—	●	●	●	—	●	—	●	—
Pseudorotalia indopacifica (Thalmann)	—	—	—	●	●	●	—	●	●	—	—
Triloculina tricarinata d'Orbigny	—	—	—	○	—	●	●	●	—	—	—
Asterorotalia inspinosa Huang	—	—	—	—	●	●	●	●	—	—	—
Calcarina hispida Brady	—	—	—	—	●	—	●	●	—	—	—
Cancris auriculus (Fichtel & Moll)	—	—	—	—	●	—	●	●	—	—	—
Cellanthus adelaidensis (Howchin & Parr)	—	—	—	—	●	●	●	●	—	—	—
Fissurina sp. 1	—	—	—	—	●	—	●	—	—	—	—
Globigerinoides sacculifer (Brady)	—	—	—	—	●	—	—	—	—	—	—
Guttulina pacifica (Cushman & Ozawa)	—	—	—	—	●	●	—	—	—	—	—
Gypsina globula (Reuss)	—	—	—	—	●	●	●	—	—	—	—
Hastigerina siphonifera (d'Orbigny)	—	—	—	—	●	—	—	—	—	—	—
Siphouvigerina proboscidea (Schwager) var. *vadescens* (Cushman)	—	—	—	—	●	●	●	●	—	—	—
Alveolinella quoyi (d'Orbigny)	—	—	—	—	—	●	—	●	—	—	—
Amphistegina cf. *lessonii* d'Orbigny	—	—	—	—	—	●	—	●	—	—	—
Amphistegina cf. *wanneriana* Fischer	—	—	—	—	—	●	●	—	—	—	—
Brizalina amygdalaeformis (Brady) *iokiensis* (Asano)	—	—	—	—	—	●	●	●	●	—	—
Caribeanella ogiensis (Matsunaga)	—	—	—	—	—	●	●	●	●	—	—
Cribroelphidium dentense sp. nov.	—	—	—	—	—	●	—	—	—	—	—
Cymbaloporetta squammosa (d'Orbigny)	—	—	—	—	—	●	●	●	—	—	—
Dendritina striata Hofker	—	—	—	—	—	●	—	●	—	—	—
Edentostomina cf. *millettii* (Cushman)	—	—	—	—	—	●	●	●	—	—	—
Elphidium cf. *fax barbarense* Nicol	—	—	—	—	—	●	—	●	—	—	—
Fissurina sp. 2	—	—	—	—	—	●	●	●	—	—	—
Fissurina sp. 3	—	—	—	—	—	●	●	—	—	—	—
Heterostegina sp.	—	—	—	—	—	●	—	—	—	—	—
Lagena elongata (Ehrenberg)	—	—	—	—	—	●	—	●	—	—	—
Marginopora cf. *vertebralis* de Blainville	—	—	—	—	—	●	—	●	—	—	—
Nummulites cf. *amplicuneatus* (Cole)	—	—	—	—	—	●	—	—	—	—	—
Nummulites tamanensis (Vaughan & Cole)	—	—	—	—	—	●	—	—	—	—	—
Oolina squamosa (Montagu)	—	—	—	—	—	●	●	—	—	—	—
Operculina bartschi Cushman	—	—	—	—	—	●	●	—	—	—	—
Peneroplis planatus (Fichtel & Moll) var. *annulata* nov.	—	—	—	—	—	●	—	—	—	—	—
Pseudomassilina australis (Cushman)	—	—	—	—	—	●	—	—	—	—	—
Pseudomassilina medioelata sp. nov.	—	—	—	—	—	●	●	—	—	—	—
	NB 9456/7	NB 9455	NB 9454	NB 9453	NB 9460	NB 9452	NB 9450	NB 9449	NB 9448	NB 9447	NB 9446

ranged in ascending stratigraphic order from left to right. ● = species present; ○ = doubtful record

	NB 9456/7	NB 9455	NB 9454	NB 9453	NB 9460	NB 9452	NB 9450	NB 9449	NB 9448	NB 9447	NB 9446
Reussella sp.	—	—	—	—	—	●	●	●	—	—	—
Sigmoidella elegantissima (Parker & Jones)	—	—	—	—	—	●	●	—	—	—	—
Spiroloculina lucida Cushman & Todd	—	—	—	—	—	●	—	●	—	●	—
Spiroloculina manifesta Cushman & Todd	—	—	—	—	—	●	●	●	●	—	—
Ammonia beccarii (Linnaeus) var. *tepida* (Cushman)	—	—	—	—	—	—	●	—	—	●	●
Anomalinoides glabratus (Cushman)	—	—	—	—	—	—	●	—	—	—	—
Bolivina sabahensis sp. nov.	—	—	—	—	—	—	●	—	—	●	—
Chrysalidinella dimorpha (Brady)	—	—	—	—	—	—	●	○	—	—	—
Cymbaloporetta bradyi (Cushman)	—	—	—	—	—	—	●	●	—	—	—
Cymbaloporetta plana (Cushman)	—	—	—	—	—	—	●	●	—	—	—
Epistomaroides polystomelloides (Parker & Jones)	—	—	—	—	—	—	●	●	—	●	—
Glandulina laevigata (d'Orbigny)	—	—	—	—	—	—	●	●	—	—	—
Globigerina bulloides d'Orbigny	—	—	—	—	—	—	●	—	—	—	—
Globigerinoides ruber (d'Orbigny)	—	—	—	—	—	—	●	●	—	—	—
Hanzawaia nipponica Asano	—	—	—	—	—	—	●	—	—	—	—
Hauerina fragilissima (Brady)	—	—	—	—	—	—	●	●	—	—	—
Lagena clavata (d'Orbigny)	—	—	—	—	—	—	●	●	—	●	—
Lagena clavata (d'Orbigny) var. *setigera* Millett	—	—	—	—	—	—	●	●	—	—	—
Lagena sp.	—	—	—	—	—	—	●	●	—	—	—
Oolina hexagona (Williamson)	—	—	—	—	—	—	●	●	—	—	—
Pararotalia calcar (d'Orbigny)	—	—	—	—	—	—	●	●	—	●	—
Parrellina hispidula (Cushman)	—	—	—	—	—	—	●	—	—	●	●
Pavonina flabelliformis d'Orbigny	—	—	—	—	—	—	●	—	—	—	—
Poroeponides cribrorepandus Asano & Uchio	—	—	—	—	—	—	●	●	—	—	—
Poroeponides lateralis (Terquem)	—	—	—	—	—	—	●	●	—	—	—
'*Pseudonodosaria*' sp.	—	—	—	—	—	—	●	●	—	—	—
Pyrgo anomala (Schlumberger)	—	—	—	—	—	—	●	—	—	●	—
Pyrgo denticulata (Brady)	—	—	—	—	—	—	●	●	—	—	—
Quinqueloculina cuvieriana d'Orbigny	—	—	—	—	—	—	●	●	—	—	—
Quinqueloculina exsculpta (Heron-Allen & Earland)	—	—	—	—	—	—	●	●	—	●	●
Rectobolivina raphana (Parker & Jones)	—	—	—	—	—	—	●	—	—	—	—
Rectobolivina striata (Schwager) var. *curta* (Cushman)	—	—	—	—	—	—	●	—	—	—	—
'*Schackoinella*' *globosa* (Millett)	—	—	—	—	—	—	●	●	—	●	—
Schlumbergerina sp.	—	—	—	—	—	—	●	—	—	—	—
Siphogenerina sp.	—	—	—	—	—	—	●	—	—	—	—
Siphoninoides echinatus (Brady)	—	—	—	—	—	—	●	—	—	●	—
Spiroloculina eximia Cushman	—	—	—	—	—	—	●	—	—	●	—
Textilina conica (d'Orbigny)	—	—	—	—	—	—	●	●	—	—	—
Triloculina cf. *oblonga* (Montagu)	—	—	—	—	—	—	●	●	—	●	—
Vertebralina striata d'Orbigny	—	—	—	—	—	—	●	●	—	—	—
Cancris sp.	—	—	—	—	—	—	—	●	—	●	—
Discorbis cf. *dimidiatus* (Parker & Jones)	—	—	—	—	—	—	—	●	—	●	—
Fissurina circularis Todd	—	—	—	—	—	—	—	●	—	—	—
Fissurina radiatomarginata (Parker & Jones)	—	—	—	—	—	—	—	●	—	—	—
Gavelinopsis sp.	—	—	—	—	—	—	—	●	—	●	—
Globigerinita glutinata (Egger)	—	—	—	—	—	—	—	●	—	—	—
Hauerina circinata Brady	—	—	—	—	—	—	—	●	—	—	—
Lagena flatulenta Loeblich & Tappan	—	—	—	—	—	—	—	●	—	—	—
Lagena gracillima (Seguenza)	—	—	—	—	—	—	—	●	—	—	—
Lagena laevis (Montagu)	—	—	—	—	—	—	—	●	—	—	—
Lagena semistriata Williamson	—	—	—	—	—	—	—	●	—	—	—
Miliolinella sp.	—	—	—	—	—	—	—	●	—	●	—
Planorbulinella larvata (Parker & Jones)	—	—	—	—	—	—	—	●	●	—	—
Pseudoeponides japonicus Uchio	—	—	—	—	—	—	—	●	—	●	—
Quinqueloculina tropicalis Cushman	—	—	—	—	—	—	—	●	●	●	●
Rectobolivina raphana (Parker & Jones) var.	—	—	—	—	—	—	—	●	—	—	—
Rosalina bradyi (Cushman)	—	—	—	—	—	—	—	●	—	●	—
? *Schlumbergerina* sp.	—	—	—	—	—	—	—	●	—	—	—
Spiroloculina communis Cushman & Todd *incisa* Cushman	—	—	—	—	—	—	—	●	—	—	—
Ammonia takanabensis (Ishizaki)	—	—	—	—	—	—	—	—	—	●	—
Globigerina quinqueloba Natland	—	—	—	—	—	—	—	—	—	●	—
Pararotalia cf. *nipponica* (Asano)	—	—	—	—	—	—	—	—	—	●	●
Spiroloculina cf. *angulata* Cushman	—	—	—	—	—	—	—	—	—	●	—
	NB 9456/7	NB 9455	NB 9454	NB 9453	NB 9460	NB 9452	NB 9450	NB 9449	NB 9448	NB 9447	NB 9446

rocks younger than late Miocene. We do not have *Ammonia yabei* (Ishizaki), the zonal fossil of Billman & Kartaadipura's oldest zone, which they date as late Miocene (? M. Miocene) (Fig. 4). We cannot, therefore, relate the Togopi Formation to any one of Billman & Kartaadipura's zones, but can only state that it is probably younger than the *Ammonia yabei* Zone, a dating which is substantiated by the post-N15 age given by our planktonic foraminifera and by the accumulated micropalaeontological evidence of the underlying formations of the Dent Group (see p. 5). Almost all the zone-fossils and other important benthic markers from every zone from *Pseudorotalia catilliformis* (late Miocene) to *Calcarina* (Pleistocene/Recent) occur together in our samples. More work is, therefore, needed before a regionally reliable benthic zonation can be erected. Nevertheless, some of Billman & Kartaadipura's marker species, together with those listed in Fig. 3, may still be of more than local value.

After this paper was completed, a single specimen of *Lepidocyclina* was discovered in sample NB 9452, but in spite of diligent searching through the remainder of the unpicked residue, no further specimens were found. Dr C. G. Adams (personal communication) has referred to it as *Lepidocyclina* (*Nephrolepidina*) aff. *multilobata* Gerth. The embryonic apparatus, he reports, is fairly primitive and not lying in the same plane as the equatorial chambers which are not, therefore, visible in the sectioned specimen. The specimen was determined only on external morphological features.

This find means either that the Togopi Formation is of late Miocene age, at least in part, or that the specimen of *Lepidocyclina* is reworked. The former alternative is not thought tenable: the geographical and stratigraphical position of the Togopi Formation (see above and Haile & Wong 1965) and the evidence of the Mollusca (see p. 3) strongly militate against any suggestion that it may be of Miocene age. We must, therefore, assume, for the present at least, that the single specimen of *Lepidocyclina* is reworked and that the Togopi is mainly Pliocene in age. It follows that some of the other larger foraminifera in NB 9452 may also be reworked and this may partly explain the discordant results of our 'Factor E' analysis on *Operculina*/*Nummulites*.

The Togopi Formation, it is concluded, is mainly of Pliocene age although its upper part could perhaps be slightly younger.

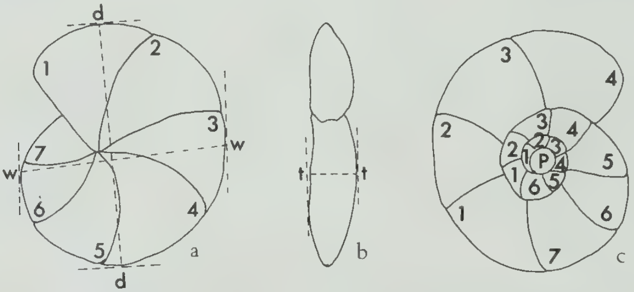


Fig. 5 A hypothetical foraminifer showing dimensions measured (Figs 5a, b: d = diameter, w = width, t = thickness) and method of counting chambers (Fig. 5a, in last whorl; Fig. 5c, in first, second and third whorls; P = proloculus).

Systematics

Synonymies have been restricted to records from the Indo–West Pacific and to important name changes or redefinitions from outside the area. The Indo–West Pacific is here defined as the area bounded by Japan and the Red Sea in the north, by Australia and New Zealand in the south, East Africa in the west and Hawaii in the east. Rare and indeterminate species, although figured, are dealt with only briefly.

We have wherever possible compared our material directly with that of other authors and extensive reference has been made to the following important collections housed in the BM(NH): H. B. Brady ('Challenger'), W. B. Carpenter, A. C. Collins, E. Heron-Allen & A. Earland, F. W. Millett and W. K. Parker & T. R. Jones. Syntypes have been borrowed, where necessary, from the U.S. National Museum.

Dimensions, given under the heading 'Variation', are the maxima for the smallest and largest specimen (Figs 5a, b) except where otherwise stated. Chamber counts in both planispiral and trochoid forms exclude the proloculus (Fig. 5c). Counts for the last whorl commence, of course, with the final chamber (Fig. 5a).

The classification followed here is that of the Treatise on Invertebrate Paleontology (Loeblich & Tappan 1964) except that the genus *Operculina* is reinstated, *Amphisorus* and *Sphaerogypsina* are regarded as junior synonyms of *Marginopora* and *Gypsina* respectively, and *Tretomphalus* is considered merely to be the planktonic reproductive phase of species of *Rosalina* and *Cymbaloporetta*. Finally, the 'post-Treatise' genus *Textilina* (Nørvang 1966) is used for two species previously referred to *Textularia*.

All figured specimens are deposited in the British Museum (Natural History), London, and their registered numbers are cited in the plate and figure explanations. A duplicate set of specimens has been deposited with the Geological Survey of Malaysia, Ipoh, Malaya.

Family **ATAXOPHRAGMIIDAE** Schwager, 1877
Subfamily **VERNEUILININAE** Cushman, 1911
Genus ***TEXTILINA*** Nørvang, 1966

Type-species: *Textularia stricta* Cushman, 1911.

Textilina conica (d'Orbigny)
Pl. 1, figs 1a, b

1839 *Textularia conica* d'Orbigny : 143; pl. 1, figs 19, 20.
1966 *Textilina conica* (d'Orbigny) Nørvang : 9; pl. 1, figs 5–7; pl. 2, fig. 8.

MATERIAL. 5 specimens. NB 9449, 9450.

VARIATION. Length 0·50–0·63 mm, width 0·72–1·08 mm, thickness 0·45–0·80 mm.

REMARKS. Apparently very variable in both length (height) and thickness of the test. A Recent suite of specimens from Darvel Bay, Sabah, in the collections of the BM(NH) shows similar variation.

This species possesses a triserial initial part and a coarsely perforate wall characteristic of *Textilina* (Nørvang 1966 : 6–9). The suprageneric position of *Textilina* and all other members of the Textulariina is now in urgent need of revision (Murray 1973).

RANGE. Pliocene (Asano 1950*b*) to Recent.

Textilina subrectangularis sp. nov.
Pl. 1, figs 2a–c

DIAGNOSIS. A moderately compressed species of *Textilina*. Chambers rarely inflated; most sutures flush, moderately inclined. Test characteristically subrectangular in apertural view.

NAME. From the shape of the test.

HOLOTYPE. BM(NH) reg. no. P50062 from sample NB 9449.

MATERIAL. 36 specimens. NB 9449, 9450, 9452, 9454.

DESCRIPTION (Holotype). Test free, agglutinating, tapering, moderately compressed, subrectangular in apertural view, slightly curved in edge view. Initial chambers subrounded, last few chambers broad and strongly arched. Sides of test almost flat, peripheries broadly rounded. Chambers 9 in each series; sutures mainly flush and difficult to discern, initially horizontal, then inclined at about 30° to the axial plane. Aperture a short rectangular slit at the base of the last chamber.

DIMENSIONS (Holotype). Length 0·70 mm, breadth 0·40 mm, thickness 0·27 mm.

VARIATION. Size range of paratypes: length 0·35–0·85 mm, breadth 0·29–0·40 mm, thickness 0·18–0·30 mm. In a few specimens the later chambers are slightly inflated and the sutures correspondingly depressed. The number of chambers varies between 8 and 10 pairs.

REMARKS. A number of specimens have been examined in thin section and by scanning electron microscopy. There was no sign of an initial planispiral coil, rather the first three chambers following the proloculus appeared in all cases to be arranged triserially, the remainder biserially. This feature, together with the observed presence of minute perforations in the wall of the test, place the species in the genus *Textilina* (Nørvang 1966).

Textilina subrectangularis sp. nov. has been compared with Heron-Allen & Earland's type-material of the Recent *Textularia foliacea* from the Kerimba Archipelago, East Africa (BM(NH) nos 1955:10:21:429–442). Both species have approximately the same number of chambers, but the former is smaller, thicker and has less inflated chambers and depressed sutures, thus lacking the foliaceous outline of the latter. Moreover, the sides of *T. subrectangularis* are characteristically flattened and the peripheries broadly rounded. *Textularia malaccaensis* Le Roy, originally described from the Miocene of Sumatra (Le Roy 1939 : 230; pl. 9, figs 4, 5), has more highly inclined sutures and is much more compressed than the present species.

Subfamily **VALVULININAE** Berthelin, 1880
Genus ***CLAVULINA*** d'Orbigny, 1826

Type-species: *Clavulina parisiensis* d'Orbigny, 1826.

Clavulina pacifica Cushman
Pl. 1, figs 3a, b

1884 *Clavulina angularis* d'Orbigny; Brady : 396; pl. 48, figs. 22–24b (*non* d'Orbigny, 1826).
? 1921 *Clavulina angularis* d'Orbigny; Cushman : 155; pl. 31, fig. 3.
1924 *Clavulina pacifica* Cushman : 22; pl. 6, figs 7–11.
1937 *Clavulina pacifica* Cushman; Cushman : 25; pl. 3, figs 17a–18b.
1952 *Clavulina pacifica* Cushman; Uchio : 151; pl. 6, figs 4a, b.
1954 *Clavulina pacifica* Cushman; Cushman, Todd & Post : 332; pl. 83, fig. 19.
1959 *Clavulina pacifica* Cushman; Graham & Militante : 32; pl. 2, figs 17a, b.
1960 *Clavulina pacifica* Cushman; Barker : 98; pl. 48, figs 22–24b (after Brady).
1964 *Clavulina pacifica* Cushman; Rocha & Ubaldo : 36; pl. 1, figs 16, 17.
1965 *Clavulina pacifica* Cushman; Moura : 14; pl. 1, fig. 6.
1970 *Clavulina pacifica* Cushman; Murray : 63 (list); figs 5A, B.

MATERIAL. 18 specimens. NB 9447, 9448, 9449, 9450, 9454.

VARIATION. Length 0·55–1·65 mm, width 0·30–0·43 mm; number of uniserial chambers 3–10.

DISTRIBUTION. *Fossil*: The only previous fossil record appears to be from the sub-Recent of northern Timor, alluvium in the 2-metre raised coastal plain (Rocha & Ubaldo 1964). *Recent*: Widespread in the western Pacific. Murray (1970) records it from the Abu Dhabi lagoon, Persian Gulf; Moura (1965) from the coast of Mozambique.

Family **NUBECULARIIDAE** Jones, 1875
Subfamily **OPHTHALMIDIINAE** Wiesner, 1920
Genus ***EDENTOSTOMINA*** Collins, 1958

Type-species: *Miliolina cultrata* Brady, 1879.

Edentostomina cf. ***millettii*** (Cushman)
Figs 6–8; Pl. 3, figs 4a, b

cf. 1898 *Miliolina durrandii* Millett (*pars*) : 268; pl. 6, figs 8–10 only.
cf. 1917 *Biloculina millettii* Cushman : 81; pl. 34, figs 4, 5.

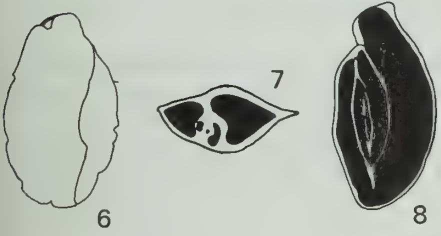
MATERIAL. 9 specimens. NB 9449, 9450, 9452.

VARIATION. Length 0·66–1·55 mm, width 0·27–0·91 mm, thickness 0·13–0·53 mm.

REMARKS. This carinate, moderately inflated species with an edentate oval aperture is unfortunately usually found broken and infilled with pyrite in the Togopi samples. The best-preserved adult specimen, however, appears to be triloculine as three chambers are visible on one side and two on the other (see Fig. 6; Pl. 3, fig. 4a). This arrangement is nevertheless neither triloculine nor typically miliolid, as can be seen from the drawing of the half-section (Fig. 7). The coiling is more or less planispiral; the chambers few, the last two being added at approximately 180°. We therefore follow Loeblich & Tappan (1964 : C448) in placing *Edentostomina* within the Ophthalmidiinae.

Of the species of *Edentostomina* so far described, the Togopi specimens are most like *E. millettii* (Cushman), though the paucity of our material precludes any certainty that it is conspecific. Cushman (1917 : 81), who introduced the name for the 'biloculine form' of *Miliolina durrandii* Millett (1898 : 268; pl. 5, figs 8–10 only), stated that the aperture was toothed, a statement which he repeated later but did not substantiate with his figure (Cushman 1932 : 66; pl. 15, fig. 4b). This anomaly was not commented on by Collins (1958 : 370), who when diagnosing his new genus considered that '. . . the main point of difference from *Triloculina* s. str. [was] the large oval and edentate aperture'.

DISTRIBUTION. The genus is widespread in the Indo-Pacific at the present day. This is possibly its first authenticated fossil record.



Figs 6–8 *Edentostomina* cf. *millettii* (Cushman). 6, P50094. Reverse side of specimen illustrated in Pl. 3, fig. 4a. Sample NB 9452. ×20. 7, P50236. Section showing the almost planispiral nature of the coil. Sample NB 9452. ×40. 8, P50237. Equatorial section. Sample NB 9450. ×20.

Subfamily **SPIROLOCULININAE** Wiesner, 1920
Genus ***SPIROLOCULINA*** d'Orbigny, 1826

Type-species: *Spiroloculina depressa* d'Orbigny, 1826.

Spiroloculina cf. ***angulata*** Cushman
Fig. 9; Pl. 1, fig. 4

cf. 1917 *Spiroloculina grata* Terquem var. *angulata* Cushman : 36; pl. 7, figs 5a, b.

MATERIAL. 3 specimens. NB 9447.

VARIATION. Length 0·85–0·90 mm, width 0·50–0·60 mm, thickness 0·20–0·23 mm. Up to 12 ribs on last chamber, number of chambers 6–10.

REMARKS. Considerable confusion exists between *S. angulata* Cushman and *S. antillarum* d'Orbigny. In 1944 Cushman & Todd redefined them, primarily on the appearance of their tests in apertural view. The chambers of the latter (1944 : 44) were said to be typically more inflated than those of the former which has rounded peripheries. *S. angulata* (1944 : 51) is thinner and, as the name implies, has an angled periphery often with a pronounced median ridge. Costation, otherwise, is similar in the two forms and the shape of the test is very variable in both.

On the strength of this dissimilarity, Cushman & Todd conclude that *S. antillarum* is restricted to the Recent of the western Atlantic (it was originally described by d'Orbigny in 1826 from

Cuba), while *S. angulata* is found widely in the Indo-Pacific. However, since their work appeared Albani (1965) has found *S. antillarum* in south-east African waters, while several authors have recorded it from the coasts of India.

As we have only one complete specimen, we are not able to clarify the situation to any great extent. We can say, however, that our form is very similar to that illustrated by Brady (1884) as *S. grata* (*non* Terquem 1878) from Shell Cove, Port Jackson, Australia, and since transferred to *S. angulata* by Barker (1960). Both Brady's figures (pl. 10, figs 22a, b) and our own, however, lack the truly angular periphery shown in the holotype (Cushman & Todd 1944 : pl. 7, fig. 18b).

Spiroloculina angulata has a fossil record back to the Pliocene (Asano 1951), whereas *S. antillarum* is known only from the Recent.

Spiroloculina communis Cushman & Todd ***incisa*** Cushman

Pl. 1, fig. 5

1921 *Spiroloculina grateloupi* d'Orbigny var. *incisa* Cushman : 397; pl. 78, fig. 5.
1944 *Spiroloculina communis* Cushman & Todd var. *incisa* Cushman; Cushman & Todd : 64; pl. 9, figs 1–3, 6.
1951 *Spiroloculina communis incisa* Cushman; Asano : 13, text-figs 89, 90.

MATERIAL. 5 specimens. NB 9449.

VARIATION. Length 0·39–0·83 mm, width 0·24–0·57 mm, thickness 0·14–0·33 mm.

REMARKS. The holotype appears to be a very large individual, about 3·7 mm long. Other specimens, however, illustrated by Cushman & Todd (1944), especially a topotype (figs 1a, b), are identical in size and appearance to those from the Togopi Formation. Evidently the size range is considerable.

Cushman (*in* Cushman & Todd 1944) transferred *incisa* as a variety to *S. communis* Cushman & Todd, from which it differs only in having the peripheral margins of the chambers raised above the succeeding chambers.

DISTRIBUTION. *Fossil*: Pliocene of Japan (Asano 1951). *Recent*: The Philippines (Cushman 1921, Cushman & Todd 1944).

Spiroloculina eximia Cushman

Pl. 1, fig. 6

1922 *Spiroloculina eximia* Cushman: 61; pl. 11, fig. 2.
1924 *Spiroloculina eximia* Cushman; Cushman : 56; pl. 21, fig. 2.
1929 *Spiroloculina eximia* Cushman; Cushman : 42; pl. 8, figs 7a, b.
1932 *Spiroloculina eximia* Cushman; Cushman : 39; pl. 10, figs 2, 3.
1944 *Spiroloculina eximia* Cushman; Cushman & Todd : 46; pl. 6, figs 36a–38b.
1956 *Spiroloculina eximia* Cushman; Bhatia : 18; pl. 1, figs 14a, b.
1964*b* *Spiroloculina eximia* Cushman; Rocha & Ubaldo : 647 (list); pl. 2, figs 7, 8.

MATERIAL. 7 specimens. NB 9447, 9450.

VARIATION. Length 0·44–0·74 mm, width 0·28–0·45 mm, thickness 0·20–0·28 mm.

DISTRIBUTION. A common species in the Recent tropical western Pacific, but known also from the west coast of India (Bhatia 1956, Rocha & Ubaldo 1964*b*). It was originally described from the Tortugas, off Florida, though further records from the Caribbean appear to be lacking. The Togopi specimens are believed to consitute the first fossil record.

Spiroloculina lucida Cushman & Todd

Pl. 1, fig. 7

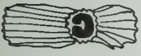
1944 *Spiroloculina lucida* Cushman & Todd : 70; pl. 9, figs 30–31b.
1951 *Spiroloculina lucida* Cushman & Todd; Asano : 15, text-figs 99, 100.
1956*a* *Spiroloculina lucida* Cushman & Todd; Asano : 68; pl. 7, figs 5a, b.

Material. 3 specimens. NB 9447, 9449, 9452.

Variation. Length 0·46–0·90 mm, width 0·30–0·59 mm, thickness 0·21–0·42 mm.

Remarks. Only the figured specimen is complete. However, enough is preserved of the others to show that the peripheral margins of the older chambers always project to form weak ridges. This feature is less apparent in the holotype (Cushman & Todd 1944 : pl. 9, fig. 31a) than in the paratype (1944 : pl. 9, fig. 30). The main difference between *S. lucida* and *S. communis* (and its subspecies) is that in typical members of the latter group the periphery is flat or more commonly concave, while in the former it is convex.

Distribution. *Fossil*: Pliocene of Pacific coast of Japan (Asano 1951). *Recent*: Western Pacific from Japan (Asano 1956*a*) southwards to south-eastern Australia (Cushman & Todd 1944).



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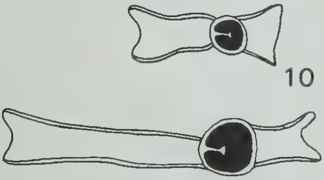

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Fig. 9 *Spiroloculina* cf. *angulata* Cushman. P50064. Apertural view of specimen figured on Pl. 1, fig. 4. Sample NB 9447. ×40.

Figs 10, 11 *Spiroloculina manifesta* Cushman & Todd. Apertural views of specimens figured on Pl. 1, figs 8, 9. Sample NB 9450. ×40. 10, P50068, megalospheric form. 11, P50069, microspheric form.

Spiroloculina manifesta Cushman & Todd

Figs 10, 11; Pl. 1, figs 8, 9

1917 *Spiroloculina canaliculata* d'Orbigny; Cushman : 30; pl. 4, figs 1–3 (*non* d'Orbigny 1846).
1921 *Spiroloculina depressa* d'Orbigny; Cushman : 394; pl. 81, fig. 2 only (*non* d'Orbigny 1826).
1921 *Spiroloculina canaliculata* d'Orbigny; Cushman : 395; pl. 80, fig. 3a, b.
1932 *Spiroloculina grateloupi* d'Orbigny; Cushman (*pars*) : 34; pl. 8, fig. 9 only (*non* d'Orbigny 1826).
1944 *Spiroloculina manifesta* Cushman & Todd : 62; pl. 8, figs 26a–28.
1951 *Spiroloculina manifesta* Cushman & Todd; Asano : 15, text-figs 101, 102.
1956*a* *Spiroloculina manifesta* Cushman & Todd; Asano : 68; pl. 7, figs 4a, b, 8a, b.

Material. 36 specimens. NB 9448, 9449, 9450, 9452.

Variation. *Megalospheric form*: length 0·40–1·12 mm, width 0·21–0·73 mm, thickness 0·10–0·25 mm; maximum number of whorls 7. *Microspheric form*: length 1·08–1·70 mm, width 0·70–1·15 mm, thickness 0·18–0·30 mm; maximum number of whorls 9.

Remarks. Considerable morphological variation exists within the Togopi specimens. The microspheric form tends to be subcircular in side view with the chambers nearly flush; the megalospheric form, on the other hand, is much narrower and often strongly concave in the central portion of the test. In both, however, the margins are keeled, giving a characteristic concave appearance to the periphery when seen in apertural view (Figs 10, 11).

Distribution. *Fossil*: Pliocene of Japan (Asano 1951). *Recent*: Cushman & Todd (1944) list its occurrence from the Red Sea and Arabian Coast eastwards to the West Pacific islands. The holotype is from the Philippines.

Subfamily **NODOBACULARIINAE** Cushman, 1927

Genus ***VERTEBRALINA*** d'Orbigny, 1826

Type-species: *Vertebralina striata* d'Orbigny, 1826.

Vertebralina striata d'Orbigny

Fig. 12

1826 *Vertebralina striata* d'Orbigny : 283, no. 1, modèle 81.

MATERIAL. 2 specimens. NB 9449, 9450.

DIMENSIONS OF FIGURED SPECIMEN. Length 0·56 mm, width 0·43 mm, thickness 0·12 mm.

REMARKS. A very variable species largely owing to the attitude of the later chambers which tend to become uncoiled and rectilinear. Our specimens, although closely coiled, are similar to many examples in the Brady 'Challenger' and Millett collections.

RANGE. Pliocene (Yabe & Asano 1937, Asano 1951*c*) to Recent.

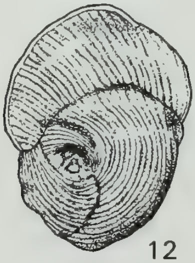

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Fig. 12 *Vertebralina striata* d'Orbigny. P50238. Side view. Sample NB 9449. ×60.

Family **MILIOLIDAE** Ehrenberg, 1839
Subfamily **QUINQUELOCULININAE** Cushman, 1917
Genus ***QUINQUELOCULINA*** d'Orbigny, 1826

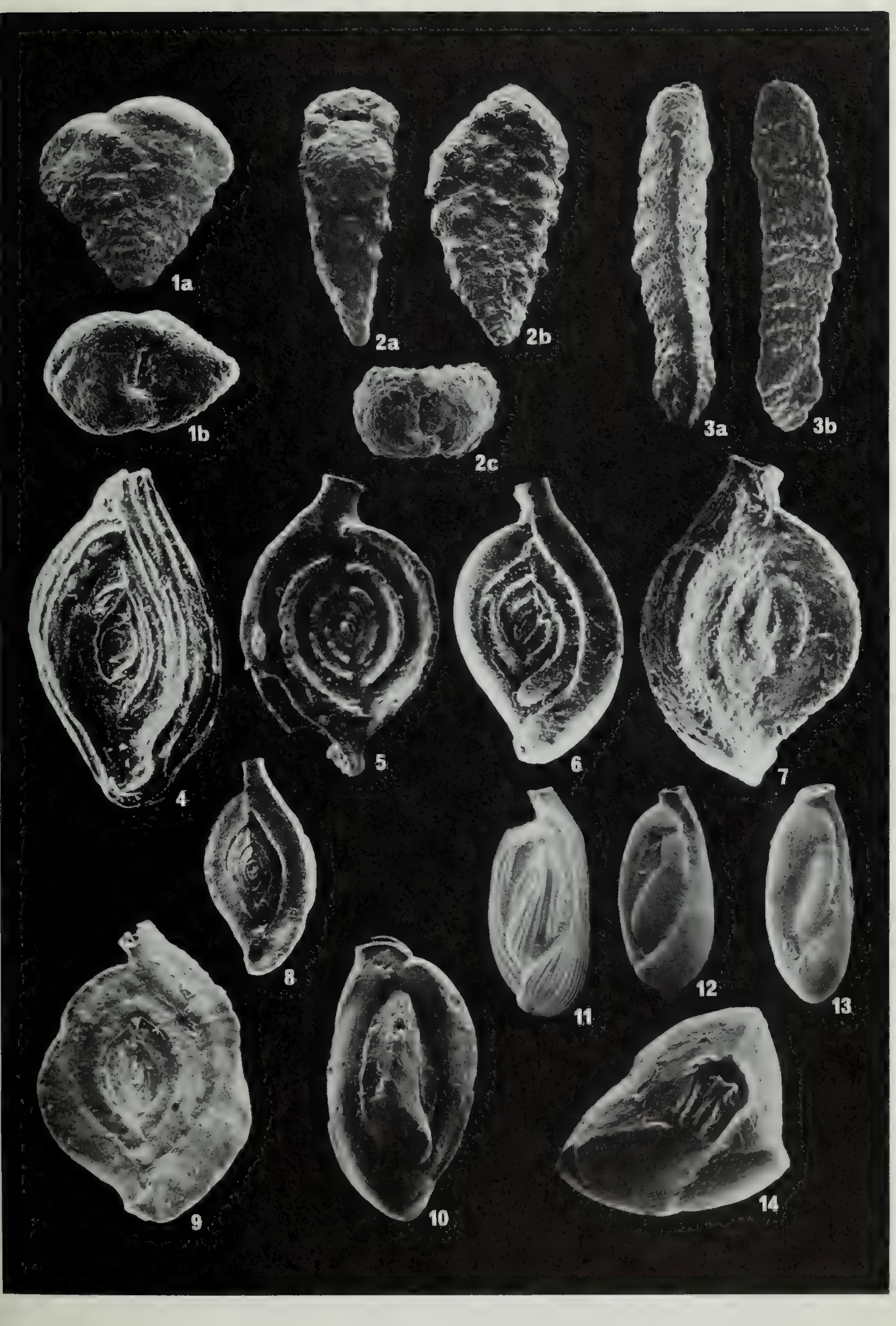
Type-species: *Serpula seminulum* Linné, 1758.

Quinqueloculina contorta d'Orbigny
Figs 13, 14; Pl. 1, fig. 10

1846 *Quinqueloculina contorta* d'Orbigny: 298; pl. 20, figs 4–6.
1951 *Quinqueloculina contorta* d'Orbigny; Asano: 3, text-figs 11–13.
1956*a* *Quinqueloculina contorta* d'Orbigny; Asano: 58; pl. 7, figs 12a–c.
1963 *Quinqueloculina contorta* d'Orbigny; Matsunaga: pl. 27, figs 9a–c.
1964*a* *Quinqueloculina contorta* d'Orbigny; Rocha & Ubaldo: 410; pl. 1, figs 1a, b.

Plate 1 Scanning Electron Micrographs

Figs 1a, b *Textilina conica* (d'Orbigny). P50061. Side and apertural views. Sample NB 9449. ×60.
Figs 2a–c *Textilina subrectangularis* sp. nov. P50062. Edge, side and apertural views. **Holotype,** sample NB 9449. ×60.
Figs 3a, b *Clavulina pacifica* Cushman. P50063. Side views. Sample NB 9449. ×35.
Fig. 4 *Spiroloculina* cf. *angulata* Cushman. P50064. Side view. Sample NB 9447. ×60. (See Fig. 9, p. 19.)
Fig. 5 *Spiroloculina communis* Cushman & Todd *incisa* Cushman. P50065. Side view. Sample NB 9449. ×60.
Fig. 6 *Spiroloculina eximia* Cushman. P50066. Side view. Sample NB 9450. ×60.
Fig. 7 *Spiroloculina lucida* Cushman & Todd. P50067. Side view. Sample NB 9452. ×60.
Figs 8, 9 *Spiroloculina manifesta* Cushman & Todd. P50068, P50069. Side views of megalospheric and microspheric forms. Sample NB 9450. ×30. (See Figs 10–11, p. 19.)
Fig. 10 *Quinqueloculina contorta* d'Orbigny. P50070. Side view. Sample NB 9452. ×60. (See Fig. 13, p. 22.)
Figs 11, 12 *Quinqueloculina exsculpta* (Heron-Allen & Earland). P50071, P50072. Side views of striate and smooth forms. Sample NB 9449. ×75.
Fig. 13 *Quinqueloculina tropicalis* Cushman. P50073. Side view. Sample NB 9449. ×75.
Fig. 14 *Quinqueloculina cuvieriana* d'Orbigny. P50074. Apertural view of large specimen; see also Pl. 2, figs 12, 13. Sample NB 9450. ×60. (See Fig. 19, p. 24.)


1a
1b
2a
2b
2c
3a
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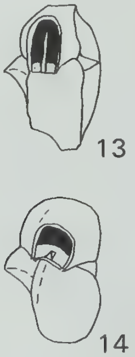
1968 *Quinqueloculina contorta* d'Orbigny; Chiji & Lopez : 110; pl. 8, figs 9a–c.
1970 *Quinqueloculina contorta* d'Orbigny; Matoba : 59; pl. 2, figs 6a, b.

Material. 11 specimens. NB 9452, ? 9453 (rock section), 9454.

Variation. Length 0·56–0·90 mm, width 0·31–0·50 mm, thickness 0·21–0·37 mm.

Remarks. Le Roy (1964 : F20; pl. 3, figs 7, 8) records *Q. contorta* from the Neogene of Okinawa, west Pacific. Because of its well-pronounced striate ornamentation, however, we hesitate to include Le Roy's species within the present synonymy.

In apertural view, the Togopi specimens have either rounded or truncate chamber peripheries (Figs 13, 14). The truncate form is very similar in appearance to that from the Recent of north-east Japan figured by Matoba (1970 : pl. 2, figs 6a, b) and closely resembles d'Orbigny's type-figure (1846 : pl. 20, figs 4–6).



Figs 13, 14 *Quinqueloculina contorta* d'Orbigny. Contrasting apertural views. 13, P50070. Specimen illustrated in Pl. 1, fig. 10. 14, P50239. Sample NB 9452. ×50.

Distribution. *Fossil*: Originally described from the Tertiary of Nussdorf in the Vienna Basin (d'Orbigny 1846) it has subsequently been recorded from the Pliocene of Japan (Asano 1951, Matsunaga 1963). *Recent*: Coasts of Japan (Asano 1956*a*, Chiji & Lopez 1968, Matoba 1970); Diu, north-west India (Rocha & Ubaldo 1964*a*).

Quinqueloculina curta Cushman

Figs 15a–17b; Pl. 2, figs 10, 11

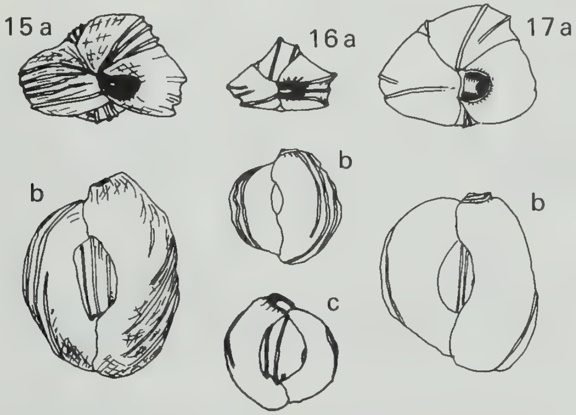
1898*a* *Miliolina cuvieriana* (d'Orbigny); Millett : 505; pl. 12, figs 2a, b (*non Quinqueloculina cuvieriana* d'Orbigny 1839).
1917 *Quinqueloculina disparalis* d'Orbigny var. *curta* Cushman : 49; pl. 14, figs 2a–c; text-fig. 30.
1921 *Quinqueloculina curta* Cushman; Cushman : 426; pl. 100, figs 1, 2.
1924 *Quinqueloculina disparalis* d'Orbigny var. *curta* Cushman; Cushman : 60; pl. 22, figs 7, 8.
1931 *Quinqueloculina curta* Cushman; Hada : 80, text-figs 33a–c.
1933 *Quinqueloculina curta* Cushman; Hofker : 98; pl. 3, figs 13–25; text-figs 19, 20.
1937 *Quinqueloculina curta* Cushman; Yabe & Asano : 114; pl. 17, figs 1–4.
1941*a* *Quinqueloculina* sp. F Le Roy: 71; pl. 5, figs 3, 4.
1941*b* *Cribrolinoides curta* (Cushman) Le Roy: 113; pl. 1, figs 1–5.
1951 *Cribrolinoides curta* (Cushman); Asano : 9, text-figs 63, 64.
1956*a* *Quinqueloculina curta* Cushman; Asano : 59; pl. 7, figs 13a, b.
1959 *Quinqueloculina curta* Cushman; Graham & Militante : 44; pl. 5, figs 9a–c.
1963 *Quinqueloculina curta* Cushman; Matsunaga : pl. 26, figs 16a–c.

Material. About 500 specimens. NB 9449, ? 9450, 9452, ? 9453, 9454, 9460.

Variation. Length 0·16–2·15 mm, width 0·55–1·62 mm, thickness 0·41–1·50 mm.

Remarks. Many of the forms illustrated by Hofker (1933 : pl. 3, figs 13–25) are present in the Togopi material. There is gradation in the larger specimens from smooth tests with rounded chambers, carinae being only poorly developed on the chamber peripheries (Figs 17a, b; Pl. 2, fig. 11), to forms with truncate, strongly carinate peripheries and even secondary reticulate ornament (Figs 15a, b; Pl. 2, fig. 10). Smaller individuals (Figs 16a–c) tend to be very similar to that figured by Graham & Militante (1959).

Cushman & Le Roy (1939) erected a new genus *Cribrolinoides*, with *Quinqueloculina curta* as the type-species, differentiated mainly by the development of a complicated ring-like cribrate aperture. Hofker (1968 : 18) has shown that this trend occurs only in some gerontic microspheric forms, the megalospheric forms having simple apertures. The present material, with the exception of one 'cribrolinoid' specimen, has relatively simple apertures with single or bifid teeth.



Figs 15a–17b *Quinqueloculina curta* Cushman. Overall variation. 15a, b, P50084. Apertural and rear views of specimen illustrated on Pl. 2, fig. 10. 16a–c, P50240. Apertural, rear and front views of small specimen with prominent carinae. 17a, b, P50085. Apertural and rear views of specimen illustrated on Pl. 2, fig. 11. All from sample NB 9449. ×15.

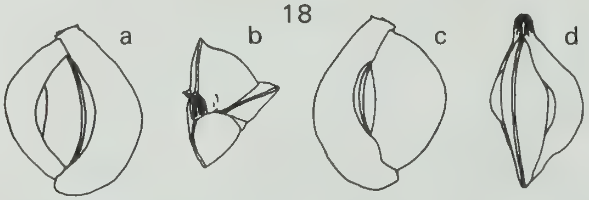
DISTRIBUTION. *Fossil*: Late Tertiary (? Pliocene) of Siberoet Island, Indonesia (Le Roy 1941*a*); Pliocene of Japan (Asano 1951, Matsunaga 1963); Pliocene (Yabe & Asano 1937) and Plio-Pleistocene (Le Roy 1941*b*) of Java. *Recent*: This species occurs widely at the present day in the west Pacific Islands from Japan to New Guinea.

Quinqueloculina cuvieriana d'Orbigny
Figs 19a–c; Pl. 1, fig. 14; Pl. 2, figs 12, 13

1839 *Quinqueloculina cuvieriana* d'Orbigny : 190; pl. 11, figs 19–21.
1884 *Miliolina cuvieriana* (d'Orbigny) Brady : 162; pl. 5, figs 12a–c.
? 1884 *Miliolina auberiana* (d'Orbigny); Brady : 162; pl. 5, figs 8, 9.
? 1917 *Quinqueloculina auberiana* d'Orbigny; Cushman : 46; pl. 12, figs 1a–c.
1921 *Quinqueloculina lamarckiana* d'Orbigny; Cushman : 418; pl. 87, figs 2a–3c; text-figs 22, 23 (*non* d'Orbigny 1839).
1931 *Quinqueloculina lamarckiana* d'Orbigny; Hada : 79, text-figs 32a–c.
1932 *Quinqueloculina lamarckiana* d'Orbigny; Cushman : 24; pl. 6, figs 2a–c.
1941*a* *Quinqueloculina* aff. *lamarckiana* d'Orbigny; Le Roy : 71; pl. 5, figs 5, 6.
1941*b* *Quinqueloculina cuvieriana* d'Orbigny; Le Roy : 112; pl. 1, figs 31–33.
1951 *Quinqueloculina lamarckiana* d'Orbigny; Asano : 5, text-figs 29–31.
1956 *Quinqueloculina lamarckiana* d'Orbigny; Bhatia : 17; pl. 2, figs 10a, b.
1956 *Quinqueloculina lamarckiana* d'Orbigny; Marks : 12, 34; pl. 9, figs 19a–c.
1956*a* *Quinqueloculina lamarckiana* d'Orbigny; Asano : 60; pl. 7, figs 17a–c; pl. 8, figs 14a–c, 17a–c; pl. 9, figs 17a, b.
1960 *Quinqueloculina lamarckiana* d'Orbigny; Barker (*pars*) : 10; pl. 5, figs 12a–c only (after Brady).
? 1960 *Quinqueloculina auberiana* d'Orbigny; Barker : 10; pl. 5, figs 8, 9 (after Brady).
1960 *Quinqueloculina lamarckiana* d'Orbigny; Chang : pl. 7, figs 5a–7b.

1961 *Quinqueloculina lamarckiana* d'Orbigny; Braga : 56; pl. 5, fig. 3.
? 1964 *Quinqueloculina carinata* d'Orbigny; Le Roy : F19; pl. 12, figs 19, 20.
1969 *Quinqueloculina lamarckiana* d'Orbigny; Resig : 77; pl. 2, fig. 14.
1970 *Quinqueloculina lamarckiana* d'Orbigny; Kim, Kim & Kim : 154; pl. ix-1, figs 7a–c.

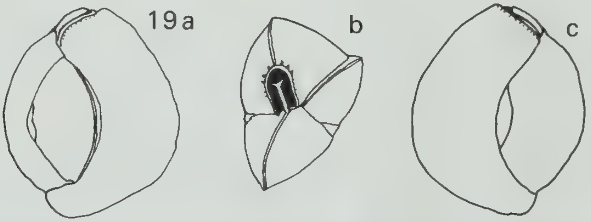
MATERIAL. 110 specimens. NB 9449, 9450.



Figs 18a–d *Quinqueloculina lamarckiana* d'Orbigny. ZF 3813. Front, apertural, rear and edge views. Note characteristic apertural neck protruding above the outline of the penultimate chamber and rounded aperture with short simple tooth. Recent, Pedro Bank, south-west of Jamaica. ×60.

VARIATION. Length 0·25–1·55 mm, breadth 0·17–1·35 mm, thickness 0·13–0·90 mm.

REMARKS. There is much confusion in the literature concerning d'Orbigny's three smooth carinate species, *Q. lamarckiana*, *Q. cuvieriana* and *Q. auberiana*, all of which were originally described from Cuba and adjacent waters.



Figs 19a–c *Quinqueloculina cuvieriana* d'Orbigny. P50074. Front, apertural (see also Pl. 1, fig. 14) and rear views. Sample NB 9450. ×35.

We have been able to examine specimens of *Q. lamarckiana* and *Q. cuvieriana* from the Pedro Bank, south-west of Jamaica, and an example of the former species from this locality, of similar size to that figured by d'Orbigny, is shown in Figs 18a–d. It has the characteristic apertural neck protruding above the outline of the penultimate chamber and a rounded aperture with a short simple tooth. Large specimens from the same sample have an even more produced neck as drawn by Le Calvez & Le Calvez (1958 : pl. 9, fig. 105). In specimens of *Q. cuvieriana*, on the other hand, the aperture is nearly flush and the tooth relatively larger, projecting above the outline of the aperture in larger specimens, when seen in lateral view. Fine striations are often developed in this form (P. Marshall, personal communication), but they can also occur in *Q. lamarckiana*, so this factor may be a variable characteristic in the group as a whole. *Q. auberiana* appears to be a rare species in the Caribbean and is not found in the Pedro Bank samples; it has an aperture like that in *Q. cuvieriana* differing according to d'Orbigny (1839 : 193) in '. . . les ondulations transversales dont elle est ornée'. We have yet to see an illustrated specimen showing this character and are thus uncertain whether *Q. cuvieriana* and *Q. auberiana* are conspecific or not. If they are, the former name has page-priority. D'Orbigny's type-figures (1839 : pl. 11, figs 19–21 and pl. 12, figs 1–3) are certainly very similar.

The situation was further complicated when Le Calvez & Le Calvez (1958 : 187) introduced *Q. viennensis* for Brady's *Q. cuvieriana* from Japan. They stated that they had examined d'Orbigny's type-specimen in Paris and found that the two were very different; this is borne out by their photograph of the type (1958 : pl. 8, fig. 90). This refigured specimen of *Q. cuvieriana* is, however, most unlike that shown by d'Orbigny in 1839, thus to prevent any confusion we are basing our identification on the original figure.

On this evidence we conclude that *Q. lamarckiana* is quite distinct from *Q. cuvierinana* and that our specimens, Brady's and all those listed in the synonymy should be referred to *Q. cuvieriana.* It is worth noting that this species has almost always been reported as *Q. lamarckiana* although in no case is the produced aperture visible.

Most larger specimens of *Q. cuvieriana* in the Togopi samples have strongly carinate peripheries, but a few are rounded or truncate. Fine longitudinal striations occur on some individuals though the majority of tests are smooth. In large specimens (Figs 19a–c; Pl. 1, fig. 14) the aperture is elongate, though always flush, and the tooth long, straight or Y or T shaped and raised above the rim. In small specimens (Pl. 2, figs 12, 13) the aperture becomes sub-rounded.

DISTRIBUTION. *Fossil*: Upper Miocene of Taiwan (Chang 1960); Miocene and Pliocene of Japan (Asano 1951); Pliocene of Okinawa (? Le Roy 1964); Late Tertiary (? Pliocene) of Siberoet Island, Indonesia and the Ewa Borehole, Hawaii (Le Roy 1941*a* and Resig 1969, respectively); Plio-Pleistocene (Le Roy 1941*b*) and Pleistocene (Marks 1956) of Java. *Recent*: Widespread in the West Pacific with reliable records also from India and East Africa.

Quinqueloculina exsculpta (Heron-Allen & Earland)
Pl. 1, figs 11, 12

1898 *Miliolina bosciana* (d'Orbigny); Millett : 267; pl. 6, figs 1a, b (*non Q. bosciana* d'Orbigny 1839).
1898 *Miliolina bosciana* (d'Orbigny) costate var., Millett : 268; pl. 6, fig. 3.
1915 *Miliolina exsculpta* Heron-Allen & Earland : 567; pl. 42, figs 23–26.
1923 *Adelosina milletti* Wiesner : 76.
1959 *Quinqueloculina bosciana* d'Orbigny; Graham & Militante : 43; pl. 5, figs 3a, b (*non* d'Orbigny 1839), = smooth forms.
1959 *Quinqueloculina poeyana* d'Orbigny; Graham & Militante : 46; pl. 5, figs 16a–c (*non* d'Orbigny 1839), = costate forms.
1968 *Quinqueloculina bosciana* d'Orbigny; Chiji & Lopez : 109; pl. 8, figs 6a, b.

MATERIAL. 53 specimens. NB 9446, 9447, 9449, 9450.

VARIATION.

	Smooth forms	*Costate forms*
Length	0·23–0·35 mm	0·26–0·50 mm
Width	0·12–0·16 mm	0·13–0·23 mm
Thickness	0·10–0·15 mm	0·11–0·19 mm

REMARKS. Wiesner (1923) erected *Adelosina milletti* for Millett's specimens of *M. bosciana* (d'Orbigny) from the Malay Archipelago. However, study of the original material and Heron-Allen & Earland's collections show that this taxon is itself a junior synonym of *Quinqueloculina exsculpta* (Heron-Allen & Earland), a costate species into which Millett's smooth forms at station 19 intergrade. Millett himself recognized a costate variety of *M. bosciana* at this locality and drew attention to the diversity of surface ornamentation in this species.

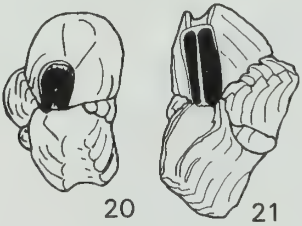
Smooth and costate forms of *Q. exsculpta* occur in the present material (NB 9449) and are figured here. They also occur in the Philippines where Graham & Militante (1959) have reported the smooth forms as *Q. bosciana* and the costate forms as *Q. poeyana.*

Although the figured syntypes of *Q. exsculpta* are unfortunately damaged, additional material from the Kerimba Archipelago and Vavau Anchorage (Tonga) in the Heron-Allen & Earland type slide collections (192, square 40; 203, square 83; 196, square 17) testifies to the fact that gradation between the smooth and ornamented forms occurs. In view of this it is surprising that Heron-Allen & Earland (1915) did not include Millett's record of *M. bosciana* in the synonymy of their new species.

DISTRIBUTION. Recorded from the Recent of the Kerimba Archipelago, East Africa, the Malay Archipelago, the Philippines, central Japan and Tonga. The Togopi material is believed to constitute the first definite fossil record.

Quinqueloculina parkeri (Brady)
Figs 20–21; Pl. 2, figs 1, 2

1858 '*Quinqueloculina* with oblique ridges' Parker : pl. 5, fig. 10 (figures).
1881 *Miliolina parkeri* Brady : 46 (description).
1884 *Miliolina parkeri* Brady; Brady : 177; pl. 7, figs 14a–c.
1915 *Miliolina parkeri* Brady; Heron-Allen & Earland : 574; pl. 43, figs 11, 12.
1917 *Quinqueloculina parkeri* (Brady) Cushman : 50; pl. 15, figs 3a–c.
1921 *Quinqueloculina parkeri* (Brady); Cushman : 440; pl. 86, figs 4a–c.
1924 *Quinqueloculina parkeri* (Brady): Cushman : 59; pl. 22, fig. 3.
1932 *Quinqueloculina parkeri* (Brady); Cushman : 25; pl. 6, figs 3, 4.
1954 *Quinqueloculina parkeri* (Brady); Cushman, Todd & Post : 333; pl. 83, fig. 23 only.
1957 *Quinqueloculina parkeri* (Brady); Todd : 286 (table); pl. 85, figs 13a–14b.
1958 *Massilina corrugata* Collins : 362; pl. 2, figs 11a–12c.
1960 *Quinqueloculina parkeri* (Brady); Barker : 14; pl. 7, figs 14a–c (after Brady).
1961 *Quinqueloculina parkeri* (Brady); Huang : 85; pl. 1, fig. 24.
1963 *Quinqueloculina parkeri* (Brady); Matsunaga : pl. 28, figs 7a–c.
1964 *Quinqueloculina parkeri* (Brady); Rocha & Ubaldo : 37; pl. 2, figs 3, 4.
1965 *Quinqueloculina parkeri* (Brady); Moura : 17; pl. 1, fig. 13.
1968 *Quinqueloculina parkeri* (Brady); Chiji & Lopez : 110; pl. 9, figs 4a, b.



Figs 20, 21 *Quinqueloculina parkeri* (Brady). Contrasting apertural views; compare with further type in Pl. 2, fig. 1. 20, P50241, sample NB 9452. 21, P50242, sample NB 9450. ×30.

MATERIAL. 29 specimens. NB 9447, 9449, 9450, 9452, 9454.

VARIATION. Length 0·30–1·20 mm, width 0·29–1·00 mm, thickness 0·20–0·57 mm.

REMARKS. In the Togopi material, the chamber peripheries of *Quinqueloculina parkeri*, when seen in apertural view, are not only acutely angled (Pl. 2, fig. 1) as in Brady's figured specimen of 1884, but also truncate (Fig. 21) or even rounded (Fig. 20). The ornament is generally well developed on the earlier visible chambers but is often sparse or absent over the last chamber, particularly in the apertural region. Brady's specimens from Honolulu and those of Parker from the Indian Ocean have been examined and show limited variation both in ornamentation and the shape of the chambers when seen aperturally; the chamber peripheries, however, are never as strongly truncated as many in the Togopi samples. Specimens identified by Millett (1898*a*) as *Q. parkeri* from the Malay Archipelago, on the other hand, are extremely variable, some of the smaller specimens resembling those of Brady while others (e.g. Millett 1898*a* : pl. 12, figs 4a, b) have crispate ornamentation in place of the regular ridges and furrows and are closer to *Miliolina kerimbatica* Heron-Allen & Earland with which his material has been synonymized (Heron-Allen & Earland 1915 : 514).

Collins (1958), in erecting this new species *Massilina corrugata*, differentiated it from *Q. parkeri* on account of its blunter periphery and because 'the characters of fully developed megalospheric specimens are those of *Massilina*' (1958 : 362). Both his holotype (pl. 2, fig. 11) and paratype (pl. 2, fig. 12) in the BM(NH), however, appear to be quinqueloculine and strongly resemble much of the Togopi material. Clearly a close investigation is needed into variation shown by Brady's species, both fossil and Recent, in the Indo-Pacific.

DISTRIBUTION. *Fossil*: Pliocene of northern Japan (Matsunaga 1963); sub-Recent alluvia of the coastal plain of northern Timor (Rocha & Ubaldo 1964). *Recent*: Originally described by Brady (1881) from Parker's specimens from the 'East Indian Seas', the species has subsequently been widely recorded in the western Pacific from central Japan (Chiji & Lopez 1968) to north-east Australia (Collins 1958). Other records include the Seychelles (Brady 1884), Inhaca Islands (Moura 1965) and the Kerimba Archipelago (Heron-Allen & Earland 1915), all off East Africa.

Quinqueloculina philippinensis Cushman
Pl. 2, figs 3–6

1917 *Quinqueloculina reticulata* (d'Orbigny); Cushman (*pars*) : 55; pl. 16, fig. 1 only.
1921 *Quinqueloculina kerimbatica* (Heron-Allen & Earland) var. *philippinensis* Cushman : 438; pl. 89, figs 2, 3.
1936 *Quinqueloculina kerimbatica* (Heron-Allen & Earland); Keijzer : 113, text-figs 15a–f (*non Miliolina kerimbatica* Heron-Allen & Earland 1915).
1936 *Quinqueloculina thalmanni* Vroman (*in* Boomgaart & Vroman) : 422, text-figs 1–5.
1937 *Quinqueloculina reticulata chitanii* Yabe & Asano : 114; pl. 17, figs. 8a–c.
1941*b* *Quinqueloculina kerimbatica* (Heron-Allen & Earland) var. *philippinensis* Cushman; Le Roy : 112; pl. 1, figs 20–22.
1959 *Triloculina kerimbatica* (Heron-Allen & Earland) var. *philippinensis* (Cushman); Graham & Militante (*pars*) : 55; pl. 8, figs 1–3c only.
1968 *Quinqueloculina* (*Miliola*) *kerimbatica* (Heron-Allen & Earland); Hofker (*pars*) : 18; pl. 3, figs 12–15 only.
1974 *Quinqueloculina philippinensis* Cushman; Ponder (*pars*) : 244; pl. 13, figs 22, 23 only.

MATERIAL. 90 specimens. NB 9449, 9450, 9452, 9454.

VARIATION. Length 0·48–1·70 mm, width 0·48–1·16 mm, thickness 0·28–0·85 mm.

REMARKS. At Togopi both generations of this species are highly variable, however a basic growth pattern is common to all; the early chambers are very prominent and the well-developed apertural neck is very characteristic. Ornamentation is a relatively coarse reticulum and there is some degree of ribbing. Some highly reticulate specimens (Pl. 2, figs 5, 6) resemble *Q. reticulata chitanii* Yabe & Asano; other specimens resemble *Q. thalmanni* Vroman. Both we consider synonyms.

Keijzer (1936) and Hofker (1968) regarded Cushman's varieties *philippinensis* and *reticulostriata* superfluous, and used only *Q. kerimbatica* (Heron-Allen & Earland). Furthermore, Hofker stated that specimens resembling var. *reticulostriata* were all megalospheric, whereas those like var. *philippinensis* were microspheric.

We have examined the syntypes of var. *philippinensis* and var. *reticulostriata* from the Philippines and have compared them with the types of *Miliolina kerimbatica* from East Africa. *Q. kerimbatica* var. *reticulostriata* (USNM no. 13488, from Albatross station D 5276) has a pronounced ridged neck, a quinqueloculine test, and ornamentation which is made up of sharp costae with large alveoli set obliquely on the final two chambers. *Q. kerimbatica* var. *philippinensis* (USNM no. 13510 from Albatross station D 5159) comprises adult forms slightly smaller than those of the preceding variety, with a similarly pronounced apertural neck and test ornament of a mainly reticulate pattern developed to a greater or lesser degree as in the Togopi material. Syntypes and topotypes of *M. kerimbatica* in the collections of the BM(NH) show a range of ornament (characteristically contorted ridges and grooves) which agrees well with Heron-Allen & Earland's figures (1915 : pl. 43, figs 13–23). The apertural neck is usually not prominent and the aperture is distinctly elongate. The test, which appears triloculine externally, is quinqueloculine in thin section. We are of the opinion that both Cushman's varieties should be separated from Heron-Allen & Earland's species (which seems to be more closely related to *Q. parkeri* (Brady)) and moreover are distinct enough to warrant separate specific status. However, juveniles have little ornament and are difficult to separate. An immature form from Togopi with neither the reticulation of *Q. philippinensis*, nor the curved alveoli of *Q. reticulostriata*, is illustrated here (Pl. 2, fig. 4).

Although Ponder (1974 and personal communication) in his review of the *Q. philippinensis* problem comes to similar conclusions to ourselves, we are still not convinced that *Q. pseudoreticulata* Parr is synonymous with *Q. philippinensis* since in the Togopi samples we cannot see gradation between the two. His pl. 13 shows many morphological types which we do not have. It may be that he has grouped together a number of different reticulate species of *Quinqueloculina*, or that this species is even more variable than the Togopi material suggests.

DISTRIBUTION. *Fossil*: Pliocene (Yabe & Asano 1937), Plio-Pleistocene (Le Roy 1941*b*) and 'Quaternary' (Vroman 1936) of Java. *Recent*: Found in the western Pacific from the Philippines to north-east Australia.

Quinqueloculina polygona d'Orbigny
Pl. 2, fig. 8

1839 *Quinqueloculina polygona* d'Orbigny : 198; pl. 12, figs 21–23.
1932 *Quinqueloculina polygona* d'Orbigny; Cushman (*pars*) : 25; pl. 6, figs 6a–c only.
1951 *Quinqueloculina polygona* d'Orbigny; Asano : 5, text-figs 32–34.
1959 *Quinqueloculina polygona* d'Orbigny; Graham & Militante : 46; pl. 6, figs 1a–c.
1961 *Quinqueloculina polygona* d'Orbigny; Huang : 85; pl. 2, figs 17, 18.
1965 *Quinqueloculina polygona* d'Orbigny; Rocha : 417; pl. 4, figs 4, 5.

MATERIAL. 62 specimens. NB 9447, 9449, 9454.

VARIATION. Length 0·35–0·90 mm, width 0·19–0·36 mm, thickness 0·15–0·43 mm.

REMARKS. Both Parr (1945) and Collins (1958) note that the cool-water species, *Quinqueloculina subpolygona*, first recorded from Victoria, Australia (Parr 1945 : 196; pl. 12, figs 2a–c) and subsequently from New South Wales (Albani 1968 : 99; pl. 7, figs 12–14), is distinct from *Q. polygona* d'Orbigny. The former appears to have a shorter, more strongly carinate and less regularly built test.

DISTRIBUTION. *Fossil*: Pliocene of Japan (Asano 1951). *Recent*: Although originally described from Cuba and Jamaica (d'Orbigny 1839) its occurrence in the Indo-Pacific is well substantiated by many workers. Records include Fiji (Cushman 1932), the Philippines (Graham & Militante 1959), western Taiwan (Huang 1961) and the Mozambique coast (Rocha 1965).

Quinqueloculina pseudoreticulata Parr
Pl. 2, fig. 9

1884 *Miliolina reticulata* (d'Orbigny); Brady : 177; pl. 9, figs 2a, b, 3 (*non Triloculina reticulata* d'Orbigny, 1826).

Plate 2 Scanning Electron Micrographs

Figs 1, 2 *Quinqueloculina parkeri* (Brady). P50075, P50076. Apertural and side views. Samples NB 9447 and NB 9450 respectively. ×60. (Compare Figs 20–21, p. 26.)

Figs 3–6 *Quinqueloculina philippinensis* Cushman. Fig. 3, P50077. Side view of 'typical specimen'. Sample NB 9449. Fig. 4, P50078. Side view of ? juvenile specimen. Sample NB 9449. Figs 5, 6, P50079, P50080. Side and apertural views of highly reticulate specimens like *Q. reticulata chitanii* Yabe & Asano. Sample NB 9450. All ×35.

Fig. 7 *Quinqueloculina sulcata* d'Orbigny. P50081. Side view. Sample NB 9450. ×35.

Fig. 8 *Quinqueloculina polygona* d'Orbigny. P50082. Side view. Sample NB 9449. ×75.

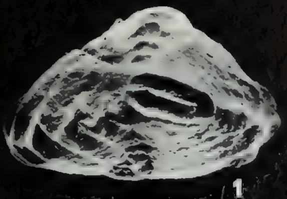
Fig. 9 *Quinqueloculina pseudoreticulata* Parr. P50083. Side view. Sample NB 9450. ×35.

Figs 10, 11 *Quinqueloculina curta* Cushman. P50084, P50085. Side views of specimens with secondary reticulation and poorly-developed carinae respectively. Sample NB 9449. ×25. (See Figs 15, 17, p. 23.)

Figs 12, 13 *Quinqueloculina cuvieriana* d'Orbigny. P50086, P50087. Side and apertural views of small carinate specimens. Sample NB 9449. ×75.

Fig. 14 *Pseudomassilina australis* (Cushman). P50088. Side view. Sample NB 9452. ×60.

Figs 15, 16 *Pseudomassilina medioelata* sp. nov. Fig. 15, P50090. Side view of immature specimen. **Paratype,** sample NB 9452. Fig. 16, P50089. Side view of adult specimen. **Holotype,** sample NB 9452. Both ×60. (See Fig. 24. p. 32.)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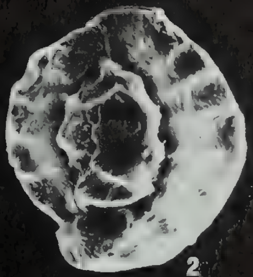
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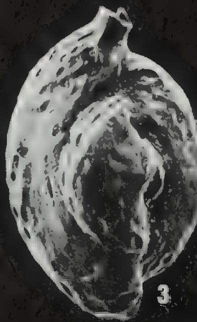
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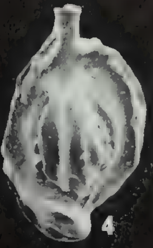
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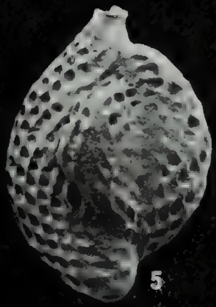
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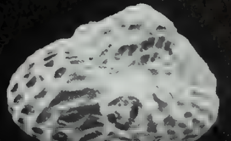
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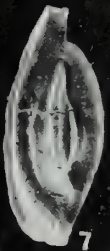
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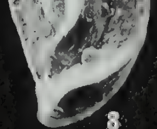
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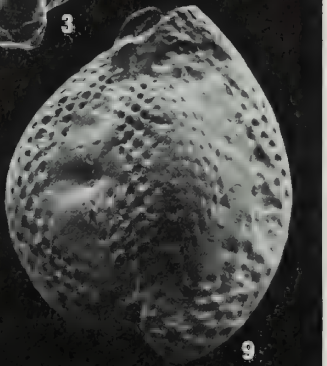
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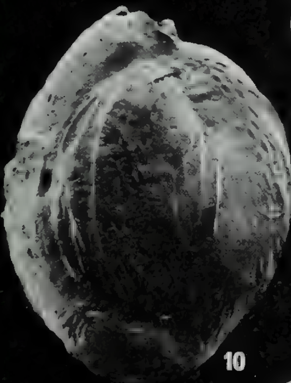
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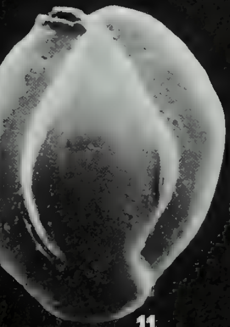
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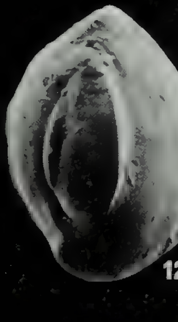
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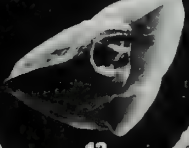
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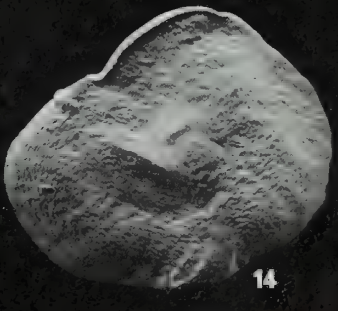
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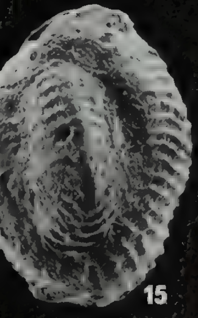
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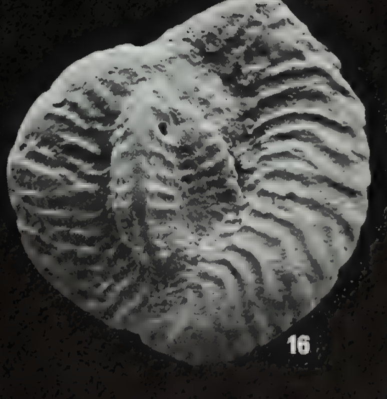
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1941 *Quinqueloculina reticulata* (d'Orbigny); Le Roy : 22; pl. 3, figs 1–3.
1941*a* *Quinqueloculina reticulata* (d'Orbigny); Le Roy : 71; pl. 5, figs 1, 2.
1941*a* *Quinqueloculina reticulata* (d'Orbigny) var. *elongata* Le Roy : 71; pl. 5, figs 13, 14.
1941 *Quinqueloculina pseudoreticulata* Parr : 305.
1951 *Quinqueloculina reticulata* (d'Orbigny); Asano : 6, text-figs 35, 36.
1958 *Quinqueloculina reticulata* (d'Orbigny); Ganapati & Satyavati : pl. 2, fig. 32.
1960 *Quinqueloculina pseudoreticulata* Parr; Barker : 18; pl. 9, figs. 2a, b, 3 (after Brady).
1964 *Quinqueloculina reticulata* (d'Orbigny); Le Roy : F19; pl. 12, figs 21, 22.
1964 *Quinqueloculina pseudoreticulata* Parr; Rocha & Ubaldo : 38; pl. 2, fig. 7.
1964*a* *Quinqueloculina pseudoreticulata* Parr; Rocha & Ubaldo : 412; pl. 1, figs 4a, b.
1964*b* *Quinqueloculina pseudoreticulata* Parr; Rocha & Ubaldo : 647 (list); pl. 2, figs 3, 4.
1965 *Quinqueloculina pseudoreticulata* Parr; Moura : 18; pl. 1, fig. 14.
1967 *Quinqueloculina pseudoreticulata* Parr; Lloyd : 88; pl. 13, figs 5a–c.
1968 *Quinqueloculina pseudoreticulata* Parr; Albani : 98; pl. 7, figs 18–20.
1968 *Quinqueloculina reticulata* (d'Orbigny); Chiji & Lopez : 110; pl. 9, figs 5a–c.
1974 *Quinqueloculina philippinensis* Cushman; Ponder (*pars*) : 244; pl. 13, figs 9, 10, 14, 15, 21, 24 only.

MATERIAL. 37 specimens. NB 9447, 9449, 9450, 9452, 9453, 9454.

VARIATION. Length 0·60–1·43 mm, width 0·35–1·16 mm, thickness 0·25–0·80 mm.

REMARKS. Normally, in the Togopi material, 3 chambers are seen on one side of the test, 4 on the other. Sometimes, however, the ratio is 3 : 3 and occasionally as many as 5 or 6 chambers have been counted on one side. The reticulate ornament is confined predominantly to the peripheral surface of each chamber, as reported by Brady (1884) and Albani (1968), the central part of each face being smooth. In larger specimens the chamber edges are broadly rounded, while in smaller specimens they are more acute.

Examination of the holotype of *Q. pseudoreticulata* and over 70 syntypes from 'Challenger' station 188, south of New Guinea, confirms that the holotype is fully exemplary of the species. Furthermore, no specimen has the test shape, produced apertural neck and coarser ornamentation of *Q. philippinensis* (Cushman). This is in conflict with the findings of Ponder (1974), who states he has evidence of a gradational series. The differences between these two species as seen in the Togopi Formation are illustrated in Pl. 2, figs 3–6, 9.

The differences between *Q. pseudoreticulata* Parr and d'Orbigny's *Triloculina reticulata* from the Mediterranean are given by Parr (1941). Cherif (1973 : pl. 14, fig. 3) has recently illustrated the latter from the Aegean Sea.

DISTRIBUTION. *Fossil*: Miocene of Okinawa, west Pacific (Le Roy 1964) and Wreck Island, north-east Australia (Lloyd 1967); Pliocene of Japan (Asano 1951); Late Tertiary of east Borneo (? Upper Miocene–Pliocene) (Le Roy 1941) and Siberoet Island, Indonesia (? Pliocene) (Le Roy 1941*a*); Sub-Recent alluvia from a raised coastal platform, northern Timor (Rocha & Ubaldo 1964). *Recent*: South of New Guinea (Brady 1884); New South Wales (Albani 1968); central Japan (Chiji & Lopez 1968); west (Rocha & Ubaldo 1964*a*, *b*) and east (Ganapati & Satyavati 1958) coasts of India; Mozambique (Moura 1965).

Quinqueloculina sulcata d'Orbigny

Pl. 2, fig. 7

1826 *Quinqueloculina sulcata* d'Orbigny : 301, no. 17.
1900 *Quinqueloculina sulcata* d'Orbigny; Fornasini : 364, text-fig. 9 (d'Orbigny's unpublished figure).
1932 *Quinqueloculina sulcata* d'Orbigny; Cushman : 28; pl. 7, figs 5–8c.
1949 *Quinqueloculina sulcata* d'Orbigny; Said : 11; pl. 1, fig. 20.
1954 *Quinqueloculina sulcata* d'Orbigny; Cushman, Todd & Post : 334; pl. 84, figs 1, 2.
? 1956*a* *Quinqueloculina* sp. Asano : 65; pl. 7, figs 18a–c.
1968 *Quinqueloculina sulcata* d'Orbigny; Chiji & Lopez : 110; pl. 9, figs 7a, b.

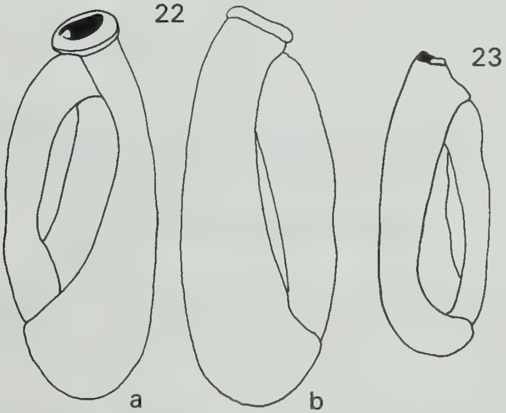
MATERIAL. 25 specimens. NB 9449, 9450, 9452, 9454.

VARIATION. Length 0·15–1·12 mm, width 0·25–0·72 mm, thickness 0·22–0·37 mm.

Distribution. Recorded in the Recent of the Red Sea (d'Orbigny 1826, Said 1949), Fiji (Cushman 1932), Marshall Is., west Pacific (Cushman, Todd & Post 1954) and Japan (Chiji & Lopez 1968, ? Asano 1956*a*). This appears to be the first fossil record.

Quinqueloculina tropicalis Cushman
Figs 22–23; Pl. 1, fig. 13

1884 *Miliolina gracilis* (d'Orbigny); Brady : 160; pl. 5, figs 3a–c (*non Triloculina gracilis* d'Orbigny, 1839).
1924 *Quinqueloculina tropicalis* Cushman : 63; pl. 23, figs 9, 10.
1959 *Quinqueloculina laevigata* d'Orbigny; Graham & Militante (*pars*) : 45; pl. 5, figs 13a–c only (*non* d'Orbigny 1826).
1960 *Quinqueloculina tropicalis* Cushman; Barker : 10; pl. 5, figs 3a–c (after Brady).
1969 *Quinqueloculina tropicalis* Cushman; Resig : 78; pl. 2, fig. 5.



Figs 22, 23 *Quinqueloculina tropicalis* Cushman. 22a, b, P50243. Front and rear views. 23, P50244. Small slender form without apertural lip. Sample NB 9449. ×95.

Material. 60 specimens. NB 9446, 9447, 9448, 9449.

Variation. Length 0·25–0·72 mm, width 0·10–0·32 mm, thickness 0·12–0·30 mm.

Remarks. Cushman (1924) referred the form figured by Brady (1884) to *Q. tropicalis* because 'it is very different from the original *Triloculina gracilis* of d'Orbigny and probably represents a species of the tropical region of the Indo-Pacific'.

The majority of the Togopi specimens have an apertural lip (Figs 22a, b) but a few do not (Fig. 23). The variation is therefore very similar to that illustrated by Cushman. All our material is quinqueloculine.

Distribution. This species has previously been described from the Recent of Papua, New Guinea (Brady 1884), the Philippines (Graham & Militante 1959) and Samoa (Cushman 1924) and from the Pleistocene of Ewa Plain, Oahu, Hawaii (Resig 1969).

Genus *PSEUDOMASSILINA* Lacroix, 1938

Type-species: *Massilina australis* Cushman, 1932.

Pseudomassilina australis (Cushman)
Pl. 2, fig. 14; Pl. 10, fig. 2

1884 *Miliolina secans* (d'Orbigny); Brady : 167; pl. 6, figs 1, 2 (*non Quinqueloculina secans* d'Orbigny 1826).

1932 *Massilina australis* Cushman : 32; pl. 8, figs 2a, b.
1936 *Massilina agglutinans* Keijzer : 120, text-figs 18, 19.
1938*a* *Pseudomassilina australis* (Cushman) Lacroix : 3, text-figs 1a–c.
1960 *Pseudomassilina australis* (Cushman); Barker : 12; pl. 6, figs 1, 2 (after Brady).

MATERIAL. 5 specimens. NB 9452.

VARIATION. Length 0·58–0·84 mm, width 0·62–0·90 mm, thickness 0·17–0·22 mm.

REMARKS. Lack of specimens precludes studies of the test variability and wall structure. However, the latter (Pl. 10, fig. 2) appears to be identical to that described and illustrated by Lacroix (1938*a*).

We suspect, following comments made by Lacroix (1938*a* : 9) and Barker (1960 : 12), that *Massilina pacificensis* Cushman, 1924 and *M. australis* Cushman [= *Miliolina secans* of Brady] are not only very similar, but also possibly synonymous. We have not seen the types, but if they were found on close study to be conspecific *M. pacificensis* would supplant *M. australis* as the name of the type-species of *Pseudomassilina.*

Keijzer's species, *M. agglutinans*, is regarded as a junior synonym; this author does not appear to have seen either of Cushman's papers cited above. Neither is included in his bibliography (1936 : 14).

DISTRIBUTION. Recent of Rarotonga, Cook Is., west Pacific (Cushman 1932), Torres Strait, off north-east Australia (Brady 1884), Cauda Bay, Vietnam and the Gulf of Aqaba, Red Sea (both Lacroix 1938*a*) and northern Java (Keijzer 1936). This is thought to be the first fossil record.

Pseudomassilina medioelata sp. nov.

Fig. 24; Pl. 2, figs 15, 16; Pl. 10, fig. 1

1959 *Pseudomassilina australis* (Cushman) var. *reticulata* (Heron-Allen & Earland); Graham & Militante : 39; pl. 3, figs 22a–c (*non Massilina secans* d'Orbigny var. *reticulata* Heron-Allen & Earland 1915).

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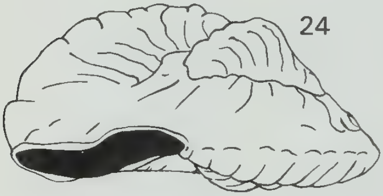


Fig. 24 *Pseudomassilina medioelata* sp. nov. P50089. Apertural view of **holotype** (see also Pl. 2, fig. 16). Sample NB 9452. ×60.

DIAGNOSIS. A *Pseudomassilina* with strong ribs and a very prominent last chamber in the quinqueloculine portion of the test.

NAME. 'Swollen in the middle', from the prominence of the final chamber of quinqueloculine portion of test.

HOLOTYPE. BM(NH) reg. no. P50089, from sample NB 9452.

MATERIAL. 11 specimens. NB 9450, 9452.

DESCRIPTION (Holotype). Test free, initially quinqueloculine, later chambers added planispirally. Early chambers prominent with subacutely-angled chamber peripheries, later planispiral chambers more flattened. Ornament of strong ribs, oblique or at right angles to the long axis of the chambers, tending to recurve towards and extend over the chamber periphery. Surface pitted. Aperture terminal, an elongate slightly sinuous toothless slit occupying the whole face.

DIMENSIONS (Holotype). Length 0·87 mm, breadth 0·82 mm, thickness 0·42 mm.

VARIATION (Paratypes). Length 0·37–1·10 mm, breadth 0·28–0·87 mm, thickness 0·25–0·42 mm.

REMARKS. In our material we have four fully-developed specimens showing the typical flattened planispiral chambers of a *Pseudomassilina* (see holotype, Pl. 2, fig. 16) and seven specimens which are not fully mature (see paratype, Pl. 2, fig. 15) and exhibit much closer coiled tests. Graham & Militante (1959) illustrate an immature form as *P. australis* var. *reticulata* (Heron-Allen & Earland).

The syntypes of *Massilina secans* var. *reticulata* Heron-Allen & Earland, from Kerimba, have been examined and found not to be conspecific with the Togopi specimens. The Kerimba variety is a typical *P. australis* (compressed and fragile) and has a fine reticulate ornament. Both the Togopi specimens and those of Graham & Militante have stronger, thicker tests and are ornamented by well-developed costae.

The wall-structure has not been fully investigated, but it has the 'granular' appearance (Pl. 10, fig. 1) described by Lacroix (1938).

DISTRIBUTION. Recent of Philippines (Graham & Militante 1959); no previous fossil record.

Genus ***PYRGO*** Defrance, 1824

Type-species: *Pyrgo laevis* Defrance, 1824.

Pyrgo anomala (Schlumberger)

Pl. 3, fig. 1

1891 *Biloculina anomala* Schlumberger: 569; pl. 11, figs 84–86; pl. 12, fig. 101.
1917 *Biloculina anomala* Schlumberger; Cushman: 79; pl. 32, figs 1a–c.
1921 *Biloculina anomala* Schlumberger; Cushman: 474; pl. 96, figs 1a–c.
1949 *Pyrgo anomala* (Schlumberger) Boomgaart: 67; pl. 5, fig. 15.
1957 *Pyrgo anomala* (Schlumberger); Daleon & Samaniego: 33; pl. 1, fig. 16.

MATERIAL. 10 specimens. NB 9447, 9450.

VARIATION. Length 0·40–0·80 mm, width 0·34–0·68 mm, thickness 0·26–0·55 mm.

DISTRIBUTION. *Fossil*: Miocene of eastern Java (Boomgaart 1949); Neogene, Panay Is., Philippines (Daleon & Samaniego 1957). *Recent*: Hawaiian Islands and the Philippines (Cushman 1917, 1921). Originally described by Schlumberger (1891) from the Mediterranean.

Pyrgo denticulata (Brady)

Pl. 3, fig. 2

1884 *Biloculina ringens* (Lamarck) var. *denticulata* Brady: 143; pl. 3, figs 4a, b, 5.
1915 *Biloculina ringens* (Lamarck) var. *denticulata* Brady; Heron-Allen & Earland: 551; pl. 40, figs. 11–13.
1917 *Biloculina denticulata* (Brady) Cushman; 80; pl. 33, figs 1a–c.
1932 *Pyrgo denticulata* (Brady) Cushman (*pars*): 62; pl. 14, figs 2a, b, 6a, b only.
1954 *Pyrgo denticulata* (Brady); Cushman, Todd & Post: 340; pl. 85, fig. 22.
1959 *Pyrgo denticulata* (Brady); Graham & Militante (*pars*): 39; pl. 4, figs 2a–c only.
1960 *Pyrgo denticulata* (Brady); Barker: 6; pl. 3, figs 4a, b, 5 (after Brady).
1961 *Pyrgo denticulata* (Brady); Braga: 87; pl. 8, figs 5, 6.
1969 *Pyrgo denticulata* (Brady); Konda: 89 (table); pl. 7, fig. 5.

MATERIAL. 3 specimens. NB 9449, 9450.

VARIATION. Length 0·57–0·73 mm, width 0·47–0·65 mm, thickness 0·35–0·57 mm.

REMARKS. These three specimens from the Togopi Formation have a maximum of 8 denticles or crenules on the aboral rim; the periphery, when seen in apertural view, is always subacute.

Previous records of this species suggest that it is a somewhat artificial group of denticulate *Pyrgo*, the development of the aperture and the shape of the test in cross section being two characters which seem to vary considerably.

DISTRIBUTION. *Fossil*: Pleistocene of central Japan (Konda 1969). *Recent*: Widespread in the western Pacific (see synonymy) with two records from the east coast of Africa, viz. Kerimba Archipelago (Heron-Allen & Earland 1915) and the Mozambique Coast (Braga 1961).

Genus *TRILOCULINA* d'Orbigny, 1826

Type-species: *Miliolites trigonula* Lamarck, 1804.

Triloculina trigonula (Lamarck)

Pl. 3, fig. 8

1804 *Miliolites* (*trigonula*) Lamarck : 351, no. 3 (description).
1807 *Miliolites trigonula* Lamarck; Lamarck : 236; pl. 17, fig. 4 (figures).
1826 *Triloculina trigonula* (Lamarck) d'Orbigny : 299, no. 1; pl. 16, figs 5–9; modèle 93.
1884 *Miliolina trigonula* (Lamarck) Brady (*pars*) : 164; pl. 3, figs 15a, b, 16 only.
1917 *Triloculina trigonula* (Lamarck); Cushman : 65; pl. 25, figs 3a, b; text-fig. 31.
1931 *Triloculina trigonula* (Lamarck); Hada : 85, text-figs 38a, b.
1932 *Triloculina trigonula* (Lamarck); Cushman : 56; pl. 13, figs 1a, b.
1936 *Triloculina trigonula* (Lamarck); Keijzer : 103, text-figs 7a–c.
1941 *Triloculina trigonula* (Lamarck); Le Roy : 22; pl. 3, figs 26–28.
1949 *Triloculina trigonula* (Lamarck); Said : 19; pl. 2, fig. 12.
1949 *Triloculina trigonula* (Lamarck); Boomgaart : 66; pl. 5, fig. 13.
1951 *Triloculina trigonula* (Lamarck); Asano : 17, text-figs 116, 117.
1954 *Triloculina trigonula* (Lamarck); Cushman, Todd & Post : 340; pl. 85, fig. 18.
1955 *Triloculina trigonula* (Lamarck); Takayanagi : pl. 1, fig. 14.
1956*a* *Triloculina trigonula* (Lamarck); Asano : 75; pl. 8, figs 5a, b.
1957 *Triloculina trigonula* (Lamarck); Todd : 288 (table); pl. 86, figs 16a, b.
1960 *Triloculina trigonula* (Lamarck); Chang : 88; pl. 7, figs 14a–15b.
1960 *Triloculina trigonula* (Lamarck); Barker : 6; pl. 3, figs 15a, b, 16 (after Brady).
1961 *Triloculina trigonula* (Lamarck); Braga : 75; pl. 7, fig. 1.
1961 *Triloculina trigonula* (Lamarck); Huang : 86; pl. 2, figs 23, 24.
1963 *Triloculina trigonula* (Lamarck); Matsunaga : pl. 30, figs 2a, b.
1964 *Triloculina trigonula* (Lamarck); Bhatia & Bhalla : 79; pl. 1, figs 5a, b.
1964*a* *Triloculina* cf. *trigonula* (Lamarck); Rocha & Ubaldo : 413; pl. 5, figs 5a, b.
1964 *Triloculina trigonula* (Lamarck); Le Roy : F20; pl. 16, figs 30, 31.
1965 *Triloculina trigonula* (Lamarck); Moura : 26; pl. 3, fig. 4.
1967 *Triloculina trigonula* (Lamarck); Lloyd : 92; pl. 14, figs 9 (? 8a, b).
1968 *Triloculina trigonula* (Lamarck); Bhalla : 382; pl. 1, figs 2a, b.
1968 *Triloculina trigonula* (Lamarck); Chiji : pl. 2, fig. 2.
1968 *Triloculina trigonula* (Lamarck); Chiji & Lopez : 113; pl. 7, figs 12a, b.
1969 *Triloculina trigonula* (Lamarck); Konda : 92 (table); pl. 5, figs 4a, b.
1969 *Triloculina trigonula* (Lamarck); Rao : 592; pl. 3, figs 21a, b.
1970 *Triloculina trigonula* (Lamarck); Matoba : 62; pl. 3, figs 3a, b.
1970 *Triloculina trigonula* (Lamarck); Bhalla : 157; pl. 20, figs 4a, b.

MATERIAL. 21 specimens. NB 9447, 9448, 9449, 9452, 9454.

VARIATION. Length 0·28–0·65 mm, width 0·19–0·53 mm, thickness 0·22–0·61 mm.

DISTRIBUTION. *Fossil*: Miocene of Taiwan (Chang 1960), eastern Java (Boomgaart 1949) and Wreck Island, north-east Australia (Lloyd 1967); Late Tertiary (? U. Miocene–Pliocene) of eastern Borneo (Le Roy 1941); Pliocene of Japan (Asano 1951, Matsunaga 1963) and Okinawa, west Pacific (Le Roy 1964); Pleistocene of Japan (Chiji 1968, Konda 1969). Originally described from the Eocene of France (Lamarck 1804, d'Orbigny 1826). *Recent*: A cosmopolitan species frequently found throughout the Indo-Pacific region at the present day.

Triloculina bradyana (Cushman)

Pl. 3, fig. 10

1884 *Miliolina fichteliana* (d'Orbigny); Brady : 169; pl. 4, figs 9a–c (*non Triloculina fichteliana* d'Orbigny, 1839).
1921 *Flintina bradyana* Cushman : 467.
1932 *Triloculina fichteliana* d'Orbigny; Cushman : 55; pl. 12, figs 6a–c.
1936 *Triloculina fichteliana* d'Orbigny; Keijzer : 106, text-figs 9a–e.
1959 *Triloculina fichteliana* d'Orbigny; Graham & Militante : 53; pl. 7, figs 10a–c.

1960 *Flintina bradyana* Cushman; Barker: 8; pl. 4, figs 9a–c (after Brady).
1964 *Flintina bradyana* Cushman; Chang: pl. 2, figs 1a, b.

MATERIAL. 13 specimens. NB 9449, 9452, ? 9453, 9454.

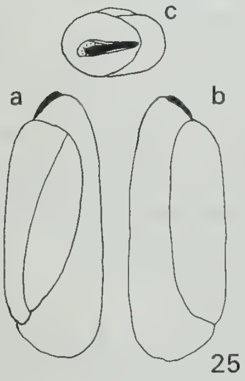
VARIATION. Length 0·61–1·50 mm, width 0·56–1·45 mm, thickness 0·45–1·14 mm.

REMARKS. We have examined specimens of *Triloculina fichteliana* from Jamaica (one of d'Orbigny's original localities) and find that they compare well with the type-figure (d'Orbigny 1839: pl. 9, figs 8–10) except that they appear to develop a small apertural flap and should therefore be referrred to the genus *Miliolinella*.

Cushman (1921) introduced *Flintina bradyana* for Brady's specimens from Japan, and with this we concur, as they, like ours, are not d'Orbigny's species. However, he included large specimens (up to 2 mm in length) from the Philippines which develop three planispiral chambers in the last whorl and a complex tooth: the two main diagnostic features of his new genus *Flintina*.

The Challenger type-material (which Cushman probably never saw) includes specimens up to 1·2 mm in length, all with a narrow simple apertural tooth and no '*Flintina*-like' coil. Since the Togopi material is also entirely triloculine and clearly conspecific with Brady's material we refer it here to *Triloculina*. All forms included in the above synonymy are triloculine.

DISTRIBUTION. *Fossil*: Miocene of Taiwan (Chang 1964). *Recent*: Japan (Brady 1884); Guam (Cushman 1932), Java (Keijzer 1936) and the Philippines (Graham & Militante 1959).



Figs 25a–c *Triloculina* cf. *oblonga* (Montagu). P50245. Specimen with terminal slit aperture in plane of coiling. Front, rear and apertural views. Sample NB 9449. ×50.

***Triloculina* cf. *oblonga* (Montagu)**
Figs 25a–c; Pl. 3, fig. 7

cf. 1803 *Vermiculum oblongum* Montagu: 522; pl. 14, fig. 9.

MATERIAL. 27 specimens. NB 9447, 9449, 9450.

VARIATION. Length 0·24–0·85 mm, width 0·10–0·36 mm, thickness 0·08–0·25 mm.

REMARKS. *Triloculina oblonga*, first described from the Recent of south-west England by Montagu (1803), has subsequently been applied to many different elongate, ovate, smooth miliolids from almost every part of the world. Of the Indo-Pacific records only a few are strictly conspecific with the Togopi specimens and it is for this reason and because of the provenance and imperfectly known nature of the original material that it has been decided to assign this species only tentatively to that of Montagu.

The present specimens are all long and thin and except for a few small quinqueloculine forms, always triloculine. In 13 individuals the aperture is rounded or elongate, never miliolinellid, and the tooth is T-shaped. In the remainder, it is a terminal slit in the plane of coiling (Figs 25a–c), filled or closed by a long narrow tooth. Apertures of this type appear to be rare in this group. They occur, however, in *Triloculina bermudezi* Acosta and *Miliolina deplanata* Rhumbler (Recent species from the Bahamas and Hawaii, respectively) and in specimens labelled *Miliolina oblonga* (Montagu) from New Caledonia, present in the collections of the British Museum (Natural History). The last-mentioned is almost certainly conspecific with our Togopi specimens.

Triloculina subgranulata Cushman
Pl. 3, fig. 6

1918 *Triloculina subgranulata* Cushman : 290; pl. 96, figs 4a–c.
1959 *Triloculina subgranulata* Cushman; Graham & Militante : 56; pl. 8, figs 11a–c.

MATERIAL. 20 specimens. NB 9447, 9449, 9454.

VARIATION. Length 0·30–0·61 mm, width 0·15–0·41 mm, thickness 0·12–0·32 mm.

REMARKS. All our specimens have the finely granular test indicated by Cushman and Graham & Militante; a few are faintly striate. The aperture in larger specimens is more elongate than in smaller forms where it tends to be rounded.

Possibly also conspecific is a Recent form figured, but not described, by Todd (1957 : pl. 86, figs 11a, b) as *Triloculina cuneata*, from Saipan, western Pacific. However, it is almost certainly not the same as Karrer's original species of that name which was described from the Neogene of Roumania in 1867.

DISTRIBUTION. *Recent*: Murray Island off north-east Australia (Cushman 1918) and the Philippines (Graham & Militante 1959). *Fossil*: This appears to be the first fossil record.

Triloculina tricarinata d'Orbigny
Pl. 3, fig. 9

1826 *Triloculina tricarinata* d'Orbigny : 299, no. 7 (description); modèle 94.
1865 *Triloculina tricarinata* d'Orbigny; Parker, Jones & Brady : 34; pl. 1, fig. 8 (after d'Orbigny's model).
1884 *Miliolina tricarinata* (d'Orbigny) Brady : 165; pl. 3, figs 17a, b.
1917 *Triloculina tricarinata* d'Orbigny; Cushman : 66; pl. 25, figs 1, 2; text-fig. 32.
1921 *Triloculina tricarinata* d'Orbigny; Cushman : 454, fig. 37 (includes unfigured var. *convexa*).
1931 *Triloculina tricarinata* d'Orbigny; Hada : 86, text-figs 39a, b.
1932 *Triloculina tricarinata* d'Orbigny; Cushman : 59; pl. 13, figs 3a, b.
1936 *Triloculina tricarinata* d'Orbigny; Keijzer : 103, text-figs 6a, b, d, e.
1941*b* *Triloculina tricarinata* d'Orbigny; Le Roy : 113; pl. 1, figs 18, 19.
1951 *Triloculina tricarinata* d'Orbigny; Asano : 17, text-figs 114, 115.
1954 *Triloculina tricarinata* d'Orbigny; Cushman, Todd & Post : 340; pl. 85, figs 15, 16.
1956 *Triloculina tricarinata* d'Orbigny; Marks : 35; pl. 10, figs 22a–c.
1956 *Triloculina tricarinata* d'Orbigny; Bhatia : 19; pl. 1, figs 16a, b.
1956*a* *Triloculina tricarinata* d'Orbigny; Asano : 73; pl. 8, figs 6a, b.
1958 *Triloculina tricarinata* d'Orbigny; Ganapati & Satyavati : 104; pl. 2, figs 38, 39.
1958 *Triloculina tricarinata* d'Orbigny; Sethulekshmi Amma : 8; pl. 1, figs 12, 13.
1959 *Triloculina tricarinata* d'Orbigny; Graham & Militante : 57; pl. 8, figs 14a, b.
1960 *Triloculina tricarinata* d'Orbigny; Barker : 6; pl. 3, figs 17a, b (after Brady).
1961 *Triloculina tricarinata* d'Orbigny; Braga : 77; pl. 7, figs 3, 4.
1963 *Triloculina tricarinata* d'Orbigny; Matsunaga : pl. 30, figs 1a, b.
1964 *Triloculina tricarinata* d'Orbigny; Le Roy : F20; pl. 3, figs 32, 33.
1964*a* *Triloculina tricarinata* d'Orbigny; Rocha & Ubaldo : 413; pl. 2, figs 6a, b.
1964*b* *Triloculina tricarinata* d'Orbigny; Rocha & Ubaldo : 647; pl. 2, figs 11, 12.
1965 *Triloculina tricarinata* d'Orbigny; Moura : 26; pl. 3, fig. 2.
1968 *Triloculina tricarinata* d'Orbigny; Antony : 38; pl. 2, figs 13a, b.
1968 *Triloculina tricarinata* d'Orbigny; Bhalla : 381; pl. 1, figs 3a, b.
1968 *Triloculina tricarinata* d'Orbigny; Chiji & Lopez : 113; pl. 7, figs 11a, b.
1968 *Triloculina tricarinata* d'Orbigny; Tewari & Kumar : 42; pl. 14, fig. 5.
1968 *Triloculina tricarinata* d'Orbigny; Hofker : 20; pl. 4, figs 7–10.
1969 *Triloculina tricarinata* d'Orbigny; Rao : 592; pl. 3, fig. 22.
1969 *Triloculina tricarinata* d'Orbigny; Konda : 92 (table); pl. 6, figs 4a, b.

MATERIAL. 152 specimens. NB 9449, 9450, 9452, ? 9453 (rock section).

VARIATION. Length 0·28–0·80 mm, width 0·21–0·59 mm, thickness 0·20–0·65 mm.

REMARKS. In the Togopi material, the chamber sides are rarely straight to gently concave as in d'Orbigny's model, but usually slightly convex. Examination of all the specimens in the Brady Collections labelled *Triloculina tricarinata* d'Orbigny from the Gulf of Suez, northern Red Sea, revealed that only a few are of this type, the others having convex sides. This is also true of Brady's Challenger material (1884). It is therefore probable that the convex-sided forms – named var. *convexa* by Cushman in 1921 – are more common than *T. tricarinata* s.s. in the Indo-Pacific and that there is intergradation in this particular feature. Furthermore, the keeled test, although smooth in the vast majority of specimens, was seen occasionally to be longitudinally costate at the proximal end of the last chamber, similar to *T. tricarinata* d'Orbigny var. *costata* Sethulekshmi Amma (1958 : pl. 1, figs 13a, b). Apertures range from triangular to oval in cross section.

DISTRIBUTION. *Fossil*: Miocene (Matsunaga 1963), Pliocene (Asano 1951) and Pleistocene (Konda 1969) of Japan; Miocene and Pliocene of Okinawa, western Pacific (Le Roy 1964); Plio-Pleistocene (Le Roy 1941*b*) and Pleistocene (Marks 1956) of Java. *Recent*: Ubiquitous in the western Pacific from Japan to the east coast of Australia. In addition it has been reported on a number of occasions from both the west and east coasts of the Indian subcontinent and Sri Lanka (Ceylon). Other records in the region comprise the Red Sea (type-locality of d'Orbigny 1826) and Mozambique (Braga 1961).

Subfamily **MILIOLINELLINAE** Vella, 1957

Genus ***MILIOLINELLA*** Wiesner, 1931

Type-species: *Vermiculum subrotundum* Montagu, 1803.

Miliolinella sp.

Pl. 3, fig. 5

MATERIAL. 12 specimens. NB 9447, 9449.

VARIATION.	5 triloculine forms	2 intermediate forms	5 quinqueloculine forms
Length	0·24–0·37 mm	0·28–0·35 mm	0·29–0·45 mm
Width	0·19–0·23 mm	0·18–0·22 mm	0·17–0·26 mm
Thickness	0·16–0·20 mm	0·12–0·19 mm	0·12–0·21 mm

REMARKS. Loeblich & Tappan (1964 : C466–8) restricted *Miliolinella* to triloculine forms, as exemplified by the type figure. Haynes (1973 : 57), however, showed that in Cardigan Bay, Wales, there is a wide range of coiling within the type-species which includes quinqueloculine forms. We therefore accept a wide concept for the genus as Wiesner had intended, and regard *Scutuloris* (for quinqueloculine forms) as superfluous.

In the Togopi material there is intergradation between triloculine and quinqueloculine forms with two specimens just showing a fourth chamber externally. In addition, the flap-like tooth is variously developed; only in a few specimens does it fully constrict the aperture. Lack of specimens of this smooth species, however, prevents a fuller investigation of its affinities.

Subfamily **MILIOLINAE** Ehrenberg, 1839

Genus ***HAUERINA*** d'Orbigny *in* de la Sagra, 1839

Type-species: *Hauerina compressa* d'Orbigny, 1846.

Hauerina circinata Brady

Figs 26a–c

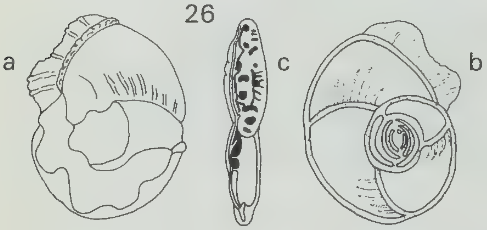
1881 *Hauerina circinata* Brady : 17 (description).
1884 *Hauerina circinata* Brady; Brady : 191; pl. 11, figs 14–16 (figures).
1975 *Hauerina circinata* Brady; Ponder : 8, text-figs 4–24 (q.v. for synonymy).

MATERIAL. 1 specimen (damaged). NB 9449.

Dimensions. Greatest diameter 0·60 mm, thickness 0·10 mm.

Remarks. *Hauerina circinata*, type-species of the monophyletic genus *Polysegmentina* Cushman (1946 : 1), has recently been extensively reviewed by Ponder (1975), based on variable Recent material from north-east Queensland. Ponder concludes that *Polysegmentina* cannot be separated from *Hauerina* either on chamber arrangement or on its possession of retral processes and sutural pores. He finds the retral process-like internal structures are not true retral processes as they do not end blindly at the chamber margins, and the sutural pores do not appear to exist. Ponder also regards *H. diversa* Cushman (1946 : 11; pl. 2, figs 16–19) as merely immature specimens of *H. circinata*.

Distribution. Probably the first fossil record from the Indo-west Pacific.



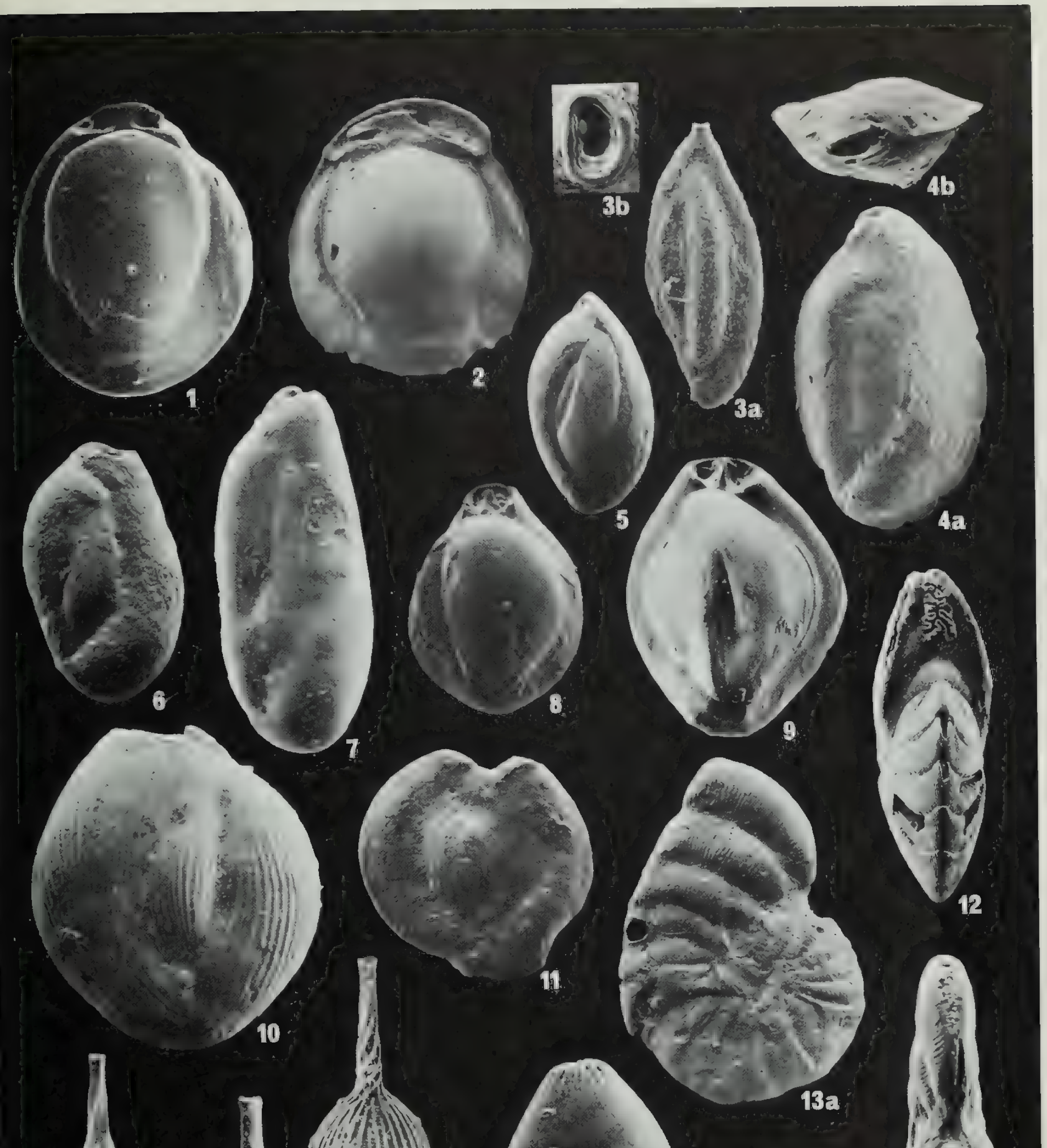
Figs 26a–c *Hauerina circinata* Brady. P50251. 26a, side view; 26b, side view in clearing medium viewed by transmitted light; 26c, apertural view. Sample NB 9449. ×55.

Hauerina fragilissima (Brady)
Pl. 3, fig. 11

1884 *Spiroloculina fragilissima* Brady : 149; pl. 9, figs 12–14.
1898*b* *Hauerina fragilissima* (Brady) Millett : 610; pl. 13, figs 8–10.
1915 *Hauerina fragilissima* (Brady); Heron-Allen & Earland : 587; pl. 46, figs 1, 2.
1924 *Hauerina fragilissima* (Brady); Cushman : 68; pl. 25, figs 2, 3.
1932 *Hauerina fragilissima* (Brady); Cushman : 42; pl. 10, fig. 9.
1946 *Hauerina fragilissima* (Brady); Cushman : 9; pl. 2, figs 1–6, 8 (after Brady, Millett).
1951 *Hauerina fragilissima* (Brady); Asano : 11, text-figs 79, 80.
1958 *Hauerina fragilissima* (Brady); Sethulekshmi Amma : 11; pl. 1, fig. 18.

Plate 3 Scanning Electron Micrographs

Fig. 1 *Pyrgo anomala* (Schlumberger). P50091. Side view. Sample NB 9450. ×70.
Fig. 2 *Pyrgo denticulata* (Brady). P50092. Side view. Sample NB 9449. ×70.
Figs 3a, b ? *Schlumbergerina* sp. P50093. Fig. 3a, side view, ×125; fig. 3b, close-up of edentate siphonate aperture, ×500. Sample NB 9449.
Figs 4a, b *Edentostomina* cf. *millettii* (Cushman). P50094. Side and apertural views. Sample NB 9452. ×30. (See Fig. 6, p. 17.)
Fig. 5 *Miliolinella* sp. P50095. Side view. Sample NB 9449. ×75.
Fig. 6 *Triloculina subgranulata* Cushman. P50096. Side view. Sample NB 9447. ×75.
Fig. 7 *Triloculina* cf. *oblonga* (Montagu). P50097. Side view. Sample NB 9450. Approx. ×60.
Fig. 8 *Triloculina trigonula* (Lamarck). P50098. Side view. Sample NB 9449. ×75.
Fig. 9 *Triloculina tricarinata* d'Orbigny. P50099. Side view. Sample NB 9449. ×60.
Fig. 10 *Triloculina bradyana* (Cushman). P50100. Side view. Sample NB 9454. ×35.
Fig. 11 *Hauerina fragilissima* (Brady). P50101. Side view. Sample NB 9450. ×60.
Figs 12–13b *Dendritina striata* Hofker. Fig. 12, P50102. Apertural (edge) view of typical specimen. Sample NB 9449. Figs 13a, b, P50103. Side and apertural view of specimen showing rectilinear trend. Sample NB 9454. All ×30.
Fig. 14 *Lagena perlucida* (Montagu). P50104. Side view. Sample NB 9449. ×80.
Fig. 15 *Lagena flatulenta* Loeblich & Tappan. P50105. Side view. Sample NB 9449. ×200.
Fig. 16 *Lagena striata* (d'Orbigny). P50106. Side view. Sample NB 9449. ×100.
Fig. 17 *Lagena laevis* (Montagu). P50107. Side view. Sample NB 9449. ×80.
Fig. 18 '*Pseudonodosaria*' sp. P50108. Side view. Sample NB 9449. ×100.
Fig. 19 '*Pseudonodosaria*' *glans* (d'Orbigny). P50109. Side view. Sample NB 9460. ×100.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1959 *Hauerina fragilissima* (Brady); Graham & Militante: 35; pl. 3, fig. 9.
1960 *Hauerina fragilissima* (Brady); Barker: 18; pl. 9, figs 12–14 (after Brady).
1963 *Hauerina fragilissima* (Brady); Matsunaga: pl. 27, figs 2a, b.
1964 *Massilina fragilissima* (Brady) Le Roy: F20; pl. 12, fig. 31.
1968 *Hauerina fragilissima* (Brady); Chiji & Lopez: 107; pl. 10, fig. 9.
1969 *Hauerina fragilissima* (Brady); Konda: 88 (table); pl. 5, fig. 6.
1969 *Heterillina fragilissima* (Brady) Resig: 67; pl. 1, fig. 9.
1975 *Hauerina fragilissima* (Brady); Ponder: 14, text-figs 28–47.

MATERIAL. 8 specimens. NB 9449, 9450.

VARIATION. Length 0·30–0·60 mm, width 0·28–0·55 mm, thickness 0·16–0·18 mm.

REMARKS. The genus *Hauerina* has been reviewed recently by Ponder (1975), based on his study of three Recent species from north Queensland, Australia. He shows that contrary to the definition of Loeblich & Tappan (1964: C470) the genus shows great variation in the apertural apparatus, chamber arrangement, number of chambers per whorl, involution of the test, inflation of the test and the development of the internal posterior longitudinal ridges.

Our specimens are for the most part similar to Brady's (1884) fig. 14. They have a prominent quinqueloculine early stage with later chambers half a whorl in length. We thus agree with Ponder, who, after studying large numbers of specimens, concluded that only in the later stages of larger individuals are there more than two chambers per whorl.

Because of the lack of variation in our material we are not able to comment on Ponder's conclusion that *Hauerina bradyi* Cushman (= *H. compressa*, *sensu* Brady and Millett) is conspecific with *H. fragilissima* (Ponder 1975: 18). Our synonymy is therefore confined to records of the latter species only.

DISTRIBUTION. *Fossil*: Pliocene (Asano 1951, Matsunaga 1963) and Pleistocene (Konda 1969) of Japan; Pliocene of Okinawa (Le Roy 1964) and Plio-Pleistocene of Hawaii (Resig 1969). *Recent*: Widespread in the East Indies and western Pacific from central Japan (Chiji & Lopez 1968) to north-west Australia (Ponder 1975). Also known with assurance from the Indian Ocean – Kerimba Archipelago, East Africa (Heron-Allen & Earland 1915) and the Travancore coast of south-west India (Sethulekshmi Amma 1958).

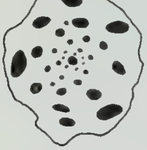
Genus *SCHLUMBERGERINA* Munier-Chalmas, 1882

Type-species: *Schlumbergerina areniphora* Munier-Chalmas, 1882.

Schlumbergerina sp.

Fig. 27

MATERIAL. 1 damaged specimen. NB 9450. Length 1·26 mm.



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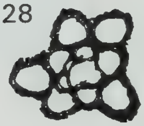

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Fig. 27 *Schlumbergerina* sp. P50252. Block section. Sample NB 9450. ×36.
Fig. 28 ? *Schlumbergerina* sp. P50246. Thin section. Sample NB 9449. ×126.

? ***Schlumbergerina*** sp.

Fig. 28; Pl. 3, figs 3a, b

MATERIAL. 9 specimens. NB 9449.

VARIATION. Length 0·26–0·46 mm, breadth 0·13–0·23 mm, thickness 0·10–0·18 mm.

REMARKS. A very small edentate form. They are juveniles of either *Ammomassilina* or *Schlumbergerina*, probably the latter since the chambers are being added in many planes (Fig. 28).

Family **SORITIDAE** Ehrenberg, 1839

Subfamily **PENEROPLINAE** Schultze, 1854

Genus ***PENEROPLIS*** de Montfort, 1808

Type-species: *Nautilus planatus* Fichtel & Moll, 1798.

Peneroplis planatus (Fichtel & Moll) var. ***annulata*** nov.

Pl. 8, fig. 8

1959 *Peneroplis discoideus* Flint; Graham & Militante: 62; pl. 9, fig. 22 (*non P. pertusus* Forskål var. *discoideus* Flint, 1899).

NAME. Referring to the distinctive annular coiling.

MATERIAL. 2 specimens (1 broken). NB 9452.

DIMENSIONS OF FIGURED SPECIMEN. Maximum diameter 3·30 mm, thickness at periphery 0·25 mm, height of chambers 0·03–0·06 mm, proloculus diameter 0·06 mm.

DESCRIPTION. Test discoidal: a peneroplid coil of 2¼ whorls comprising 35–38 undivided chambers, flaring strongly in the later part, followed by up to 10 completely annular chambers. Surface finely striate. Aperture, a single row of pores on the outer face of the last chamber.

REMARKS. Both Cole (1965) and Hofker (1971) illustrated and described specimens of *Peneroplis discoideus* from the Caribbean showing various stages of cyclical growth. Cole, however, shows quite convincingly that specimens assigned by various authors not only to this species but also to '*Orbitolites orbitolitoides*' and '*Sorites marginalis*', to name but two, are in fact a single species referable to *Peneroplis proteus* d'Orbigny. All have subepidermal partitions within the chambers, smooth tests, and are demonstrably (Cole 1965 : 14) '. . . a continuous series in which there is progressive thickening and differential deposition of the test wall, and in which the terminal chambers become annular'.

The Togopi specimens have a striate ornament and do not develop subepidermal partitions even in the final chambers. They cannot, therefore, be referred to *P. proteus*, but must be considered, if Cole's thesis is accepted, an annular form of the Indo-Pacific striate flabelliform species *Peneroplis planatus* (Fichtel & Moll). Graham & Militante figure a specimen (1959 : pl. 9, fig. 12), almost certainly striate, in which cyclical chambers are not fully developed. They consider (1959 : 62) it to be a juvenile form of *P. discoideus* (Flint). This is, as far as we are aware, the only other record of the annular form being reported in *P. planatus*.

Because this form is rare, and as no typical specimens of *Peneroplis* were found in the Togopi sediments, it has not been possible to study its specific variation. We hesitate, therefore, either to consider it worthy of separate status or, at the other extreme, to be merely conspecific. Instead, for the meantime, we have given it a varietal name, *annulata*.

DISTRIBUTION. The only previous record is a Recent one from north-central Philippines (Graham & Militante 1959).

Genus ***DENDRITINA*** d'Orbigny, 1826

Type-species: *Dendritina arbuscula* d'Orbigny, 1826.

Dendritina striata Hofker

Pl. 3, figs 12, 13a, b

1951 *Dendritina striata* Hofker : 234, text-figs 12–14.

MATERIAL. 29 specimens. NB 9449, 9452.

VARIATION. Maximum diameter 1·02–2·10 mm, thickness 0·45–0·75 mm. Height of apertural face 0·45–0·90 mm, width of apertural face 0·30–0·50 mm. Number of chambers in last whorl 17–22.

REMARKS. The Togopi specimens closely resemble those described by Hofker (1951). Tests are usually closely coiled, almost involute and, in side view, virtually undistinguishable from Hofker's (1951) text-fig. 12a. The umbilical region is flat or slightly depressed and the sutures heavy with very thick septal walls. The chamber walls, on the other hand, are relatively fragile and often broken. Scanning electron microscopy has confirmed that the longitudinal striae are indeed 'real pits, fused together', as observed by Hofker (1951). Nevertheless, similar striae also occur in related species.

A few specimens tend to uncoil in the adult stage (Pl. 3, figs 13a, b). In most mature specimens the aperture is highly dendritic (Pl. 3, fig. 12), but in a few, including those with some degree of uncoiling, it becomes drawn out and subdivided into separate openings.

DISTRIBUTION. The present fossil record complements Hofker's Recent material from eastern Borneo and the Moluccas.

Subfamily **SORITINAE** Ehrenberg, 1839
Genus ***MARGINOPORA*** de Blainville, 1830

Type-species: *Marginopora vertebralis* de Blainville, 1830.

Marginopora cf. ***vertebralis*** de Blainville
Pl. 8, fig. 6

cf. 1830 *Marginopora vertebralis* de Blainville : 337.
cf. 1834 *Marginopora vertebralis* de Blainville; de Blainville : 412; pl. 69, figs 6a–c (*Marginopore vertébral* in plate explanation).

MATERIAL. 2 specimens. NB 9449, 9452.

DIMENSIONS OF FIGURED SPECIMEN. Maximum diameter 1·40 mm, thickness 0·30 mm.

REMARKS. In these pyritized, poorly-preserved specimens, the proloculus is connected to the reniform second chamber by a flexostyle. Annular chambers, at first arcuate but later hexagonal in shape, follow immediately. There are two rows of alternating pores on the periphery. We follow Cole (1954, 1965) in regarding *Amphisorus* as a junior synonym of *Marginopora*.

RANGE. The stratigraphical range of *M. vertebralis* s.l. is Lower Miocene to Recent (Adams 1970 : 119).

Family **ALVEOLINIDAE** Ehrenberg, 1839
Genus ***ALVEOLINELLA*** Douvillé, 1906

Type-species: *Alveolina quoyi* d'Orbigny, 1826.

Alveolinella quoyi (d'Orbigny)
Pl. 8, fig. 11

1826 *Alveolina quoii* d'Orbigny : 307; pl. 17, figs 11–13.
1856 *Alveolina boscii* (Defrance); Carpenter : 552; pl. 28, figs 23, 24; pl. 29, figs 4–9 (*non Oryzaria boscii* Defrance, 1820).
1884 *Alveolina boscii* (Defrance); Brady : 222; pl. 17, figs 7–12.
1906 *Alveolinella quoyi* (d'Orbigny) Douvillé : 58.
1908 *Alveolina boscii* (Defrance); Chapman : 151; pl. 2, figs 1–3; pl. 3, figs 4, 5.
1921 *Alveolina boscii* (Defrance); Cushman : 487; pl. 99, figs 2–5.
1930 *Alveolinella quoyi* (d'Orbigny); Hofker : 166; pl. 41, figs 6–8; pl. 63, figs 1–11; pl. 64, figs 1–6.
1933 *Alveolinella quoyi* (d'Orbigny); Cushman : 68; pl. 19, fig. 10.
1954 *Alveolinella quoii* (d'Orbigny); Todd & Post : 558; pl. 202, figs 5, 8.
1958 *Alveolinella quoii* (d'Orbigny); Cole : 767; pl. 240, figs 16–25.
1959 *Alveolinella quoii* (d'Orbigny); Graham & Militante : 65; pl. 10, fig. 12.
1960 *Alveolinella quoyi* (d'Orbigny); Barker : 34; pl. 17, figs 7–12 (after Brady).
1963 *Alveolinella quoii* (d'Orbigny); Coleman : 10; pl. 1, fig. 1.
1976 *Alveolinella quoyi* (d'Orbigny); Matsumaru : 422; pl. 5, fig. 1.

MATERIAL. 181 specimens. NB 9449, 9452.

VARIATION. Length 4·7 to over 12·0 mm (specimen broken), thickness 1·3–2·5 mm.

DISTRIBUTION. *Fossil*: Neogene (Upper Miocene – ? Tg) of Bikini and Eniwetok Atolls (Todd & Post 1954 and Cole 1958, respectively); Pliocene of the Solomon Islands (Coleman 1963); Pleistocene of the Ryukyu (Nansei Shoto) Islands (Matsumaru 1976). See also Adams (1970 : 108, 109). *Recent*: Commonly found today in the shallow shelf seas of the tropical East Indies from the Philippines to north-east Australia.

Family **NODOSARIIDAE** Ehrenberg, 1838
Subfamily **NODOSARIINAE** Ehrenberg, 1838
Genus ***LAGENA*** Walker & Jacob *in* Kanmacher, 1798

Type-species: *Serpula* (*Lagena*) *sulcata* Walker & Jacob, 1798.

Lagena clavata (d'Orbigny)
Pl. 8, fig. 3

1846 *Oolina clavata* d'Orbigny : 24; pl. 1, figs 2, 3.
? 1865 *Lagena sulcata* (Walker & Jacob) var. *distomapolita* Parker & Jones (*pars*) : 357; pl. 18, fig. 8 only.
1949 *Lagena gracillima* (Seguenza); Said : 21; pl. 2, fig. 28 (*non Amphorina gracillima* Seguenza, 1862).
1951*e* *Lagena clavata* (d'Orbigny) Asano : 29, text-fig. 128.
1955 *Lagena clavata* (d'Orbigny); Takayanagi : pl. 1, fig. 30.
? 1959 *Lagena sulcata* (Walker & Jacob) var. *distomapolita* Parker & Jones; Graham & Militante : 68; pl. 10, fig. 19.
1963 *Lagena clavata* (d'Orbigny); Matsunaga : pl. 31, fig. 6.

MATERIAL. 60 specimens. NB 9447, 9449, 9450.

VARIATION. Length 0·45 to over 0·72 mm (broken specimen), maximum breadth 0·11–0·18 mm.

REMARKS. These specimens are typically shaped like Greek amphorae, with the greatest width below mid-point and the apertural end produced into a long neck with a terminal phialine lip. The base of the test has a single spine or a number of smaller spines. Many specimens in the Togopi samples become more elongate and pointed distally, thus resembling those assigned to the variety '*distomapolita*' by Parker & Jones (1865) and Graham & Militante (1959). However, they never develop the aboral tube as in *L. gracillima* (Seguenza), neither do they become as inflated as those figured as *L. clavata* by Cushman (1913 : 9; pl. 2, fig. 2) and Hada (1931 : 103, text-fig. 57).

DISTRIBUTION. *Fossil*: Pliocene of Japan (Asano 1951*e*, Matsunaga 1963). It was originally described from the Tertiary of the Vienna Basin (d'Orbigny 1846). *Recent*: Records of this species from the Indo-Pacific are few. Certainly conspecific are those from the Red Sea (Said 1949) and Japan (Takayanagi 1955) and possibly those from north-east Australia (Parker & Jones 1865) and the Philippines (Graham & Militante 1959).

Lagena clavata (d'Orbigny) var. ***setigera*** Millett
Figs 29–37

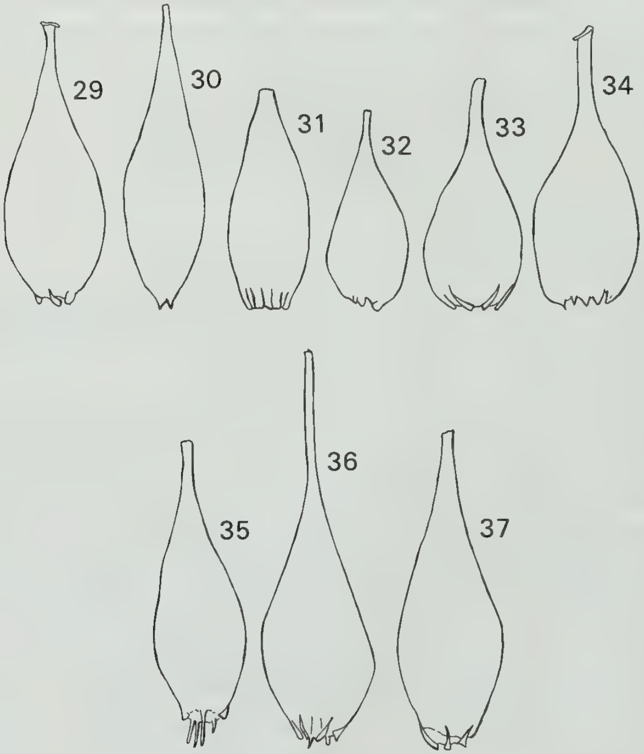
1884 *Lagena laevis* (Montagu) var.; Brady : 455; pl. 56, fig. 30.
1901*a* *Lagena clavata* (d'Orbigny) var. *setigera* Millett : 491; pl. 8, figs 9a, b.
1933 *Lagena perlucida* (Montagu); Cushman : 20; pl. 4, figs 6a–8b (*non Vermiculum perlucidum* Montagu, 1803).
1950 *Lagena perlucida* (Montagu) var.; Cushman & McCulloch : 343; pl. 46, figs 3a–4b.
1951*e* *Lagena perlucida* (Montagu); Asano : 31, text-figs 137, 138.
1959 *Lagena perlucida* (Montagu) var. of Cushman & McCulloch; Graham & Militante : 68; pl. 10, fig. 17.

1960 *Lagena laevis* (Montagu) var.; Barker : 116; pl. 56, fig. 30 (after Brady).
1968 *Lagena perlucida* (Montagu) var. of Cushman & McCulloch; Antony : 55; pl. 3, fig. 22.
1974 *Lagena oceanica* Albani : 37; pl. 1, figs 7, 10, 11.

MATERIAL. 76 specimens. NB 9449, 9450.

VARIATION. Length 0·17–0·42 mm, maximum breadth 0·09–0·13 mm.

REMARKS. This variant differs from *Lagena clavata* (d'Orbigny) in developing fine spines or wings, or both, from a moderately truncate base.



Figs 29–37 *Lagena clavata* (d'Orbigny) var. *setigera* Millett. Showing variation in shape and ornament. 29–34, P50253. Togopi sample NB 9449. ×80. 35–37, ZF3823–ZF3825. Recent, station 5, blue ooze, Malay Archipelago. ×120.

Although Millett's figured syntype cannot be recognized we have examined his residues from the Malay Archipelago and find that this species is common in the blue ooze at station 5 (Durrand 1898). Figs 35–37 show some typical specimens from this locality, while Figs 29–34 illustrate the range of variation in Togopi sample NB 9449. It is clear that the delicately 'setose' form figured by Millett (1901*a*) is rare and susceptible to damage; usually the rounded end of the test is ornamented by short costae or minute wings as in *Lagena oceanica* Albani.

As Albani (1974) rightly states, this form has often been wrongly referred to *L. perlucida*. He therefore erected a new species, *L. oceanica*, without apparently realizing that a valid taxon already existed.

DISTRIBUTION. *Fossil*: Pliocene of Japan (Asano 1951*e*). *Recent*: Hong Kong (Brady 1884), the Malay Archipelago (Millett 1901*a*), Fiji (Cushman 1933), the Philippines (Graham & Militante 1959), south-west coast of India (Antony 1968) and New South Wales, Australia (Albani 1974).

Lagena elongata (Ehrenberg)

Pl. 8, fig. 5

1844 *Miliola elongata* Ehrenberg: 274 (description).
1854 *Miliola elongata* Ehrenberg; Ehrenberg: pl. 25, fig. 1 (figure).
1884 *Lagena elongata* (Ehrenberg) Brady: 457; pl. 56, fig. 29.
1901*a* *Lagena elongata* (Ehrenberg); Millett: 492; pl. 8, fig. 10.
1913 *Lagena elongata* (Ehrenberg); Cushman: 12; pl. 1, figs 5a, b.
1938*c* *Lagena elongata* (Ehrenberg); Asano: 217; pl. 27, fig. 37 only.
1951*e* *Lagena elongata* (Ehrenberg); Asano: 30, text-fig. 132.
1956 *Lagena elongata* (Ehrenberg); Asano: 31; pl. 5, figs 15–17 only.
1960 *Lagena elongata* (Ehrenberg); Barker: 116; pl. 56, fig. 29 only (after Brady).
1963 *Lagena elongata* (Ehrenberg); Matsunaga: pl. 31, fig. 7.
1964 *Lagena elongata* (Ehrenberg); Rocha & Ubaldo: 57; pl. 4, fig. 4.

MATERIAL. 6 specimens, mostly broken. NB 9449, 9452.

VARIATION. Length 0·68–0·91 mm, maximum breadth 0·07–0·10 mm.

REMARKS. The tube-like test of this form appears in the literature to encompass many more shapes than exhibited by the present material which in every case is very similar to the type-figure. The synonymy, therefore, has been restricted to elongate cylindrical forms with nearly parallel sides for a considerable distance. Preservation of the oral and suboral necks is not commonly reported – usually they are broken back – and the apertural phialine lip seen in Pl. 8, fig. 5 is rare even in Recent material.

DISTRIBUTION. *Fossil*: Neogene of Timor (Rocha & Ubaldo 1964), Neogene and Pliocene of Japan (Matsunaga 1963 and Asano 1951*e*, respectively). The age of Ehrenberg's original material from Kurdistan is not known. *Recent*: Papua (Brady 1884), Malay Archipelago (Millett 1901*a*) and Japanese waters (Cushman 1913, Asano 1938*c* and 1956).

Lagena flatulenta Loeblich & Tappan

Pl. 3, fig. 15

1953 *Lagena flatulenta* Loeblich & Tappan: 60; pl. 11, figs 9, 10.

MATERIAL. 2 specimens. NB 9449.

DIMENSIONS OF FIGURED SPECIMEN. Length 0·24 mm, width 0·15 mm.

RANGE. Previously recorded only from Recent deposits.

Lagena gracillima (Seguenza)

Pl. 8, fig. 4

1862 *Amphorina gracillima* Seguenza: 51; pl. 1, fig. 57.
1884 *Lagena gracillima* (Seguenza) Brady (*pars*): 456; pl. 56, figs 25, 26 only.
1913 *Lagena gracillima* (Seguenza); Cushman: 11; pl. 1, figs 4a, b.
? 1937 *Lagena elongata* (Ehrenberg); Yabe & Asano: 118, text-fig. 15 (? *non* Ehrenberg, 1844).
1960 *Lagena gracillima* (Seguenza); Barker: 116; pl. 56, figs 25, 26 only (after Brady).

MATERIAL. 31 specimens. NB 9449.

VARIATION. Length 0·98 to over 1·72 mm (specimen broken), breadth 0·13–0·25 mm.

REMARKS. Our concept of this species is based on the appearance of our specimens, of which Pl. 8, fig. 4 shows a typical example. Brady's figures (1884: pl. 56) and a number of other records not included above suggest, however, that there may be greater variation particularly in the shape of the central inflated part of the test.

DISTRIBUTION. *Fossil*: First described from the Upper Miocene of Sicily, the only previous record from the Indo-Pacific appears to be that of Yabe & Asano (1937) from the Pliocene of western Java; this lack of records may be due to the fragility of the test. *Recent*: New Guinea and Kerguelen Island, south Indian Ocean (Brady 1884) and Japan (Cushman 1913).

Lagena laevis (Montagu)
Pl. 3, fig. 17

1784 *Serpula* (*Lagena*) *laevis ovalis* Walker & Boys : 3; pl. 1, fig. 9.
1803 *Vermiculum laeve* Montagu : 524.
1913 *Lagena laevis* (Montagu) Cushman : 5; pl. 1, figs 3a–c; pl. 38, fig. 5.
1931 *Lagena laevis* (Montagu); Hada : 102, text-fig. 56.
1933 *Lagena laevis* (Montagu); Cushman : 19; pl. 4, figs 5a, b.
1937 *Lagena laevis* (Montagu); Yabe & Asano : 118, text-fig. 7.
1951*e* *Lagena laevis* (Montagu); Asano : 31, text-fig. 135 only.
1956 *Lagena laevis* (Montagu); Asano : 29; pl. 5, figs 6, 7.
1959 *Lagena laevis* (Montagu); Graham & Militante : 67; pl. 10, figs 15, 16.
1963 *Lagena laevis* (Montagu); Matsunaga : pl. 31, fig. 10.
1970 *Lagena laevis* (Montagu); Kim : 106 (table); pl. 1, fig. 9.

MATERIAL. 41 specimens. NB 9449.

VARIATION. Length 0·19–0·45 mm, maximum breadth 0·09–0·25 mm.

REMARKS. We have attempted to assemble a synonymy of the species in the Indo-west Pacific region, based on the variation seen in our material and the appearance of the type-figure. In *Lagena laevis* the unornamented subglobular to inflated ellipsoidal chamber merges slowly into a usually short neck. In *L. flatulenta* Loeblich & Tappan (see Pl. 3, fig. 15 and p. 45), which is often confused with the present species, the long slender neck is quite distinct from the almost globular chamber.

None of the specimens referred by Brady (1884 : pl. 56, figs 7–14, 30) to *L. laevis* resemble the type and are not included.

DISTRIBUTION. *Fossil*: Pliocene of Japan (Asano 1951*e*, Matsunaga 1963) and Java (Yabe & Asano 1937). *Recent*: Japan (Cushman 1913, Hada 1931 and Asano 1956) and the Korean Yellow Sea (Kim 1970). The species was originally described from the south coast of England (Walker & Boys 1784).

Lagena perlucida (Montagu)
Pl. 3, fig. 14

1803 *Vermiculum perlucidum* Montagu : 525; pl. 14, fig. 3.
1858 *Lagena vulgaris* var. *semistriata* Williamson : 6; pl. 1, fig. 9 (*non L. striata* (Montagu) var. β *semistriata* Williamson, 1848).
1931 *Lagena sulcata* (Walker & Jacob) var. *interrupta* Williamson; Hada : 110, text-fig. 66 (*non L. striata* (Montagu) var. α *interrupta* Williamson, 1848).
1963 *Lagena sulcata laevicostata* Cushman & Gray; Matsunaga : pl. 31, fig. 16.
1971 *Lagena perlucida* (Montagu); Murray : 85; pl. 33, figs 1–3.
1973 *Lagena perlucida* (Montagu); Haynes : 86; pl. 12, fig. 5.

MATERIAL. 99 specimens. NB 9449, 9450, 9452, 9454, 9460.

VARIATION. Length 0·32–0·52 mm, maximum breadth 0·18–0·23 mm.

REMARKS. The test is subglobular to subtriangular in shape, the greatest width being just above the base. It is ornamented by 10–17 strong longitudinal ribs some of which are long, others short. In many specimens some of the longer ribs pass up into the neck where they either run longitudinally or spirally. At the base of the test the ribs become denticulate.

Murray (1971) and Haynes (1973) have elucidated the morphology of *V. perlucidum* Montagu. It should no longer be confused with *L. semistriata* (p. 47) and *L. clavata* var. *setigera* (p. 43), but records of Montagu's species outside British waters now need verification. The citations of Hada (1931) and Matsunaga (1963) given above are probably conspecific, while the following three species from North America are all very similar to *L. perlucida*:

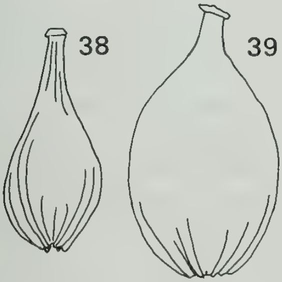
1957*a* *Lagena saccata* Todd : 231; pl. 28, fig. 12 [from the Neogene of Alaska].
1946 *Lagena sulcata* Walker & Jacob var. *laevicostata* Cushman & Gray : 68; pl. 12, figs 13, 14 [from the Pliocene of California].

1946 *Lagena pliocenica* Cushman & Gray var. *timmsana* Cushman & Gray : 68; pl. 12, figs 15–17 [from the Pliocene of California].

DISTRIBUTION. The records of Hada and Matsunaga are from the Recent and Pliocene of Japan, respectively. Now that this species has been redefined it may prove to be widespread in the Indo-Pacific.

Lagena semistriata Williamson
Figs 38, 39

1848 *Lagena striata* (Montagu) var. β *semistriata* Williamson : 14; pl. 1, figs 9, 10.
1931 *Lagena semistriata* Williamson; Hada : 105, text-fig. 60.
1933 *Lagena semistriata* Williamson; Cushman : 32; pl. 8, figs 1a, b.
1937 *Lagena semistriata* Williamson; Yabe & Asano : 118, text-fig. 3.
1938*c* *Lagena semistriata* Williamson; Asano (*pars*) : 217; pl. 25, fig. 25; pl. 27, fig. 44; pl. 29, fig. 29 only.
1941*b* *Lagena semistriata* Williamson; Le Roy : 114; pl. 3, fig. 22.
1944 *Lagena semistriata* Williamson; Le Roy : 22; pl. 1, fig. 14.
1951*e* *Lagena perlucida* (Montagu); Asano : 31, text-figs 137, 138 (*non Vermiculum perlucidum* Montagu 1803).
1956 *Lagena* cf. *perlucida* (Montagu); Asano : 35; pl. 5, fig. 38.
? 1958 *Lagena semistriata* Williamson; Sethulekshmi Amma : 57; pl. 2, figs ? 87b, c.
1973 *Lagena semistriata* Williamson; Haynes : 87; pl. 12, fig. 6; pl. 13, fig. 4.



Figs 38, 39 *Lagena semistriata* Williamson. 38, P40247. Type (b). × 100. 39, P50248. Type (a). × 125. Both from sample NB 9449.

MATERIAL. 44 specimens. NB 9449.

VARIATION. Length 0·20–0·36 mm, maximum breadth 0·09–0·22 mm.

REMARKS. Two forms are recognizable in sample NB 9449. Type (a) comprises subglobular forms with longitudinal striae confined to the basal third of the test (Fig. 39), while type (b) includes more elongate forms with longitudinal striae which are either confined to the basal part of the test or also occur on the neck (Fig. 38). This species differs from *Oolina striata* d'Orbigny in being more pear-shaped, having fewer striae (maximum of 30 against 60), a shorter, stouter neck and a more prominent phialine apertural lip. Following Haynes' (1973) description and excellent illustration of a specimen of *L. semistriata* from Britain we have no hesitation in placing our specimens in this species. Formerly, particularly in the North Atlantic, it has often been confused with *L. perlucida* (Montagu).

DISTRIBUTION. *Fossil*: Miocene of Sumatra (Le Roy 1944); Pliocene of Japan (Asano 1951*e*) and Pliocene and Plio-Pleistocene of Java (Yabe & Asano 1937 and Le Roy 1941*b*, respectively). *Recent*: Originally described from the coasts of Britain (Williamson 1848) this species is found widely in the Indo-Pacific at the present day.

Lagena striata (d'Orbigny)
Pl. 3, fig. 16

1839*b* *Oolina striata* d'Orbigny : 21; pl. 5, fig. 12.
1932 *Lagena striata* (d'Orbigny) Heron-Allen & Earland : 366; pl. 10, figs 10–12.

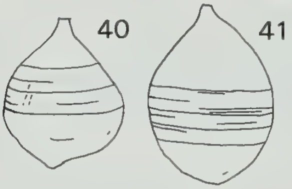
1937 *Lagena striata* (d'Orbigny); Yabe & Asano : 118, text-fig. 1.
1938*c* *Lagena striata* (d'Orbigny); Asano : 217; pl. 27, fig. 26; pl. 29, fig. 28.
1956 *Lagena striata* (d'Orbigny); Asano : 33; pl. 5, figs 28, 29.

MATERIAL. 99 specimens. NB 9449, 9450, 9452, 9454, 9460.

VARIATION. Length 0·40–0·56 mm, maximum breadth 0·14–0·25 mm.

REMARKS. *Lagena striata* was first described from the Falkland Islands by d'Orbigny (1839*b*) and was redescribed and better illustrated by Heron-Allen & Earland (1932) from the same area. The globular to subspherical test is ornamented by a great many striae (50–60) some of which run spirally round the neck. There are many incorrect records of *L. striata* from the Indo-Pacific, most of which relate to *L. substriata* Williamson or *L. sulcata* (Walker & Jacob). The latter have recently been reillustrated from the type-area by Murray (1971) and Haynes (1973).

DISTRIBUTION. *Fossil*: Pliocene of Java (Yabe & Asano 1937) and Japan (Asano 1938*c*). *Recent*: Off Japan (Asano 1956).



Figs 40, 41 *Lagena* sp. Side views. P50249, P50250. Sample NB 9449. ×70.

Lagena sp.
Figs 40, 41

MATERIAL. 18 specimens. NB 9449, 9450.

VARIATION. Length 0·25–0·35 mm, maximum breadth 0·19–0·26 mm.

REMARKS. A globular or subglobular form with a very short neck, ornamented by faint horizontal bands or ridges and sometimes also weak longitudinal striae. Similar forms have been recorded by a number of authors (notably Yabe & Asano 1937 : 118, text-fig. 4, and Le Roy 1941 : 29; pl. 3, fig. 104) as *Lagena globosa* (Montagu), but they appear to lack the horizontal bands. The present specimens are also more inflated than those originally described by Montagu from the British Isles.

Genus ***PSEUDONODOSARIA*** Boomgaart, 1949

Type-species: *Glandulina discreta* Reuss, 1850.

'Pseudonodosaria' glans (d'Orbigny)
Fig. 42; Pl. 3, fig. 19

1791 *Nautilus* (*Orthoceras*) *comatus* Batsch (*pars*) : 1, 4; pl. 1, figs 2c, d only.
1826 *Nodosaria* (*Glanduline*) *glans* d'Orbigny : 252, no. 2; modèle 51.
1865 *Nodosaria* (*Glandulina*) *glans* d'Orbigny; Parker, Jones & Brady : 27; pl. 1, fig. 3 (after d'Orbigny's model).
1902 *Nodosaria* (*Glandulina*) *comata* (Batsch); Millett : 512; pl. 11, fig. 2.
1902 *Nodosaria* (*Glandulina*) *laevigata* d'Orbigny; Millett : 509; pl. 11, figs 1a, b (*non* d'Orbigny, 1826).
1921 *Nodosaria* (*Glandulina*) *laevigata* d'Orbigny var. *striatula* Cushman : 186; pl. 33, fig. 12.
1944 *Pseudoglandulina glans* (d'Orbigny) Le Roy : 20; pl. 1, fig. 21.
1959 *Rectoglandulina glans* (d'Orbigny) Graham & Militante : 70; pl. 10, figs 26a–27b.

MATERIAL. 33 specimens. NB 9449, 9450, 9454, 9460.

VARIATION. Length 0·25–0·62 mm, breadth 0·20–0·43 mm.

REMARKS. Batsch (1791) figured two distinct striate species under *Nautilus* (*Orthoceras*) *comatus*. Parker, Jones & Brady (1865), reviewing Batsch's work, applied the name *Nodosaria comata* only to the elongate form (1791 : pl. 1, figs 2a, b); to the short stout form they assigned d'Orbigny's name *Nodosaria* (*Glandulina*) *glans*, represented by his model 51.

In the Togopi samples this completely uniserial species is generally ornamented by fine longitudinal striae and small spines on the early chambers. However, specimens from the Millett Collection (Station 12, Malay Archipelago – see Durrand 1898) suggest that considerable variation may occur. Some striate specimens are hispid, others not (Millett 1902 : pl. 11, fig. 2), while even other hispid specimens are non-striate (the *Nodosaria* (*Glandulina*) *laevigata* of Millett 1902 : pl. 11, figs 1a, b). The presence of a few non-striate spinose individuals in our material suggests that gradation occurs between hispid and non-hispid forms as well as between striate and smooth forms.

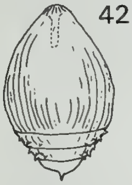


Fig. 42 '*Pseudonodosaria*' *glans* (d'Orbigny). Side view of finely striate hispid specimen showing entosolenian tube. P50254. Sample NB 9449. ×75.

The generic position of the species presents some difficulty. The entosolenian tube (always present in unbroken specimens) suggests that it should be referred to the Glandulinidae, but *Glandulina* is initially biserial (Loeblich & Tappan 1964 : C537); the uniserial *Pseudonodosaria*, on the other hand, does not appear to have an internal tube. If the type-species of *Pseudonodosaria* does not possess an entosolenian tube then a new genus will have to be erected for those forms with uniserial chambers, radial apertures and entosolenian tubes.

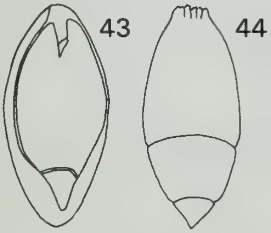
Distribution. *Fossil*: Miocene of Sumatra (Le Roy 1944). *Recent*: Malay Archipelago (Millett 1902) and the Philippines (Cushman 1921, Graham & Militante 1959). The species was originally described from the Adriatic shores of Italy (Batsch 1791, d'Orbigny 1826).

'*Pseudonodosaria*' sp.

Figs 43–44; Pl. 3, fig. 18

Material. 8 specimens. NB 9449, 9450.

Variation. Length 0·50–0·85 mm, breadth 0·25–0·45 mm.



Figs 43, 44 '*Pseudonodosaria*' sp. 43, P50255. Acid preparation showing entosolenian tube. Sample NB 9449. ×55. 44, P50256. Side view. Sample NB 9450. ×55.

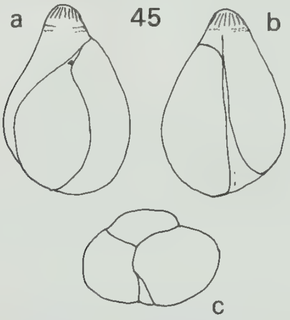
Remarks. An elongate smooth form with entosolenian tube. For further remarks on the genus see under '*Pseudonodosaria*' *glans* (d'Orbigny), above.

Family **POLYMORPHINIDAE** d'Orbigny, 1839
Subfamily **POLYMORPHININAE** d'Orbigny, 1839
Genus ***GUTTULINA*** d'Orbigny *in* de la Sagra, 1839

Type-species: *Polymorphina* (*Guttuline*) *communis* d'Orbigny, 1826.

Guttulina pacifica (Cushman & Ozawa)
Figs 45a–c

1884 *Polymorphina elegantissima* Parker & Jones; Brady (*pars*) : 566; pl. 72, figs 14, 15 only (*non* Parker & Jones 1865).
1907 *Polymorphina elegantissima* Parker & Jones; Chapman : 132; pl. 10, fig. 3.
1928 *Sigmoidella* (*Sigmoidina*) *pacifica* Cushman & Ozawa : 19; pl. 2, fig. 13.
1929 *Sigmoidina pacifica* (Cushman & Ozawa) Cushman & Ozawa : 77; pl. 16, figs 12a–13c.
1930 *Guttulina* (*Sigmoidina*) *pacifica* (Cushman & Ozawa) Cushman & Ozawa : 50; pl. 37, figs 3–5c.
1951*b* *Guttulina* (*Sigmoidina*) *pacifica* (Cushman & Ozawa); Asano : 5, text-figs 24–26.
1956 *Guttulina* (*Sigmoidina*) *pacifica* (Cushman & Ozawa) var. *ishizakii* Chang : 120; pl. 4, figs 11a–16b.
1956 *Guttulina* (*Sigmoidina*) *pacifica* (Cushman & Ozawa); Chang : 120; pl. 4, figs 17–20.
1960 *Guttulina* (*Sigmoidina*) *pacifica* (Cushman & Ozawa); Barker : 150; pl. 72, figs 14, 15 (after Brady).
1963 *Guttulina* (*Sigmoidina*) *pacifica* (Cushman & Ozawa); Matsunaga : pl. 34, figs 1a, b.
1964 *Guttulina pacifica* (Cushman & Ozawa); Le Roy : F27; pl. 11, figs 25, 26.



Figs 45a–c *Guttulina pacifica* (Cushman & Ozawa). P50257. Front, rear and basal views. Sample NB 9452. ×55.

MATERIAL. 24 specimens, NB 9452, 9460.

VARIATION. Length 0·30–0·55 mm, breadth 0·22–0·35 mm, thickness 0·22–0·35 mm.

REMARKS. We have dissected a number of specimens and find the basic chamber arrangement to be approximately quinqueloculine, not sigmoidal, with each chamber extending further from the base and strongly overlapping the previous one. Dependent on this degree of overlap the chambers visible on the exterior are either 4 : 3 or 3 : 3. Because of the nature of the coiling this species should be referred to *Guttulina*, rather than *Sigmoidella* (see Loeblich & Tappan 1964 : C533).

DISTRIBUTION. *Fossil*: Miocene of Okinawa (Le Roy 1964); Miocene and younger sediments of Taiwan (Chang 1956); ? Upper Miocene/Pliocene of Japan (Matsunaga 1963); Pliocene of Japan (Asano 1951*b*). *Recent*: West Pacific from Japan (Cushman & Ozawa 1929) to south-east Australia (Chapman 1907).

Genus *SIGMOIDELLA* Cushman & Ozawa, 1928

Type-species: *Sigmoidella kagaensis* Cushman & Ozawa, 1928.

Sigmoidella elegantissima (Parker & Jones)
Fig. 46; Pl. 8, fig. 7

1865 *Polymorphina elegantissima* Parker & Jones : 438 (table).
1870 *Polymorphina elegantissima* Parker & Jones; Brady, Parker & Jones (*pars*) : 231; pl. 40, figs 15b, c only.
1884 *Polymorphina elegantissima* Parker & Jones; Brady (*pars*) : 566; pl. 72, figs 12, ? 13 only.
1913 *Polymorphina elegantissima* Parker & Jones; Cushman : 90; pl. 38, figs 1a–c.
1921 *Polymorphina elegantissima* Parker & Jones; Cushman : 267; pl. 54, figs 1, 2.
1929 *Sigmoidella elegantissima* (Parker & Jones) Cushman & Ozawa : 76; pl. 16, figs 10, 11a, b.
1930 *Sigmoidella elegantissima* (Parker & Jones); Cushman & Ozawa : 140; pl. 39, figs 1a–c.

1937 *Sigmoidella bakomensis* Yabe & Asano : 102; pl. 18, fig. 8.
1960 *Sigmoidella elegantissima* (Parker & Jones); Barker : 150; pl. 72, figs 12, ? 13 (after Brady).
1960 *Sigmoidella bakomensis* Yabe & Asano; Chang : pl. 13, figs 12–13b.
1965 *Sigmoidella elegantissima* (Parker & Jones); Hedley, Hurdle & Burdett : 20; pl. 6, fig. 20.
1975 *Sigmoidella* sp. Billman & Kartaadipura : 306; pl. 1, fig. 7.

MATERIAL. 13 specimens. NB 9450, 9452.

VARIATION. Length 0·58–1·35 mm, breadth 0·33–1·00 mm, thickness 0·18–0·65 mm.

REMARKS. The Togopi specimens compare well with the types of *Polymorphina elegantissima* Parker & Jones from Storm Bay, Tasmania, and other specimens from south-east Australia in the Parker Collection. The only exception is that figured by Brady, Parker & Jones (1870 : pl. 40, fig. 15a) which, as indicated by Hedley, Hurdle & Burdett (1965 : 20) is much larger and is poorly preserved. It was this specimen from Melbourne which was considered to belong to *Sigmoidella kagaensis* by Cushman & Ozawa (1930 : 141).

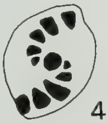

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Fig. 46 *Sigmoidella elegantissima* (Parker & Jones). P50183. Block section. Sample NB 9450. ×20.

DISTRIBUTION. *Fossil*: There are no previous illustrations of this species under the name *S. elegantissima.* However, specimens of *Sigmoidella* sp. of Billman & Kartaadipura (1975) from the Pliocene of the Kutei Basin, eastern Borneo, have been verified by us as belonging to this species. We also regard *S. bakomensis* Yabe & Asano as no more than a variant and thus the stratigraphical range probably extends back to the Miocene – Miocene of Java and Taiwan (Yabe & Asano 1937 and Chang 1960, respectively). *Recent*: Common in the warmer latitudes of the western Pacific from the Philippines (e.g. Cushman 1921) to Tasmania (e.g. Cushman 1913) and the North Island of New Zealand (Hedley, Hurdle and Burdett 1965).

Family **GLANDULINIDAE** Reuss, 1860

Subfamily **GLANDULININAE** Reuss, 1860

Genus ***GLANDULINA*** d'Orbigny *in* de la Sagra, 1839

Type-species: *Nodosaria* (*Glanduline*) *laevigata* d'Orbigny, 1826.

Glandulina laevigata (d'Orbigny)

Fig. 47

1826 *Nodosaria* (*Glanduline*) *laevigata* d'Orbigny : 252, no. 1; pl. 10, figs 1–3.
1930 *Glandulina laevigata* (d'Orbigny) Cushman & Ozawa : 143; pl. 40, figs 1a, b.
1933 *Glandulina laevigata* (d'Orbigny); Cushman : 41; pl. 9, figs 14a, b.
1941 *Glandulina laevigata* (d'Orbigny); Le Roy : 29; pl. 2, fig. 87.
1941*b* *Glandulina laevigata* (d'Orbigny); Le Roy : 115; pl. 3, figs 42, 43.
1944 *Glandulina laevigata* (d'Orbigny); Le Roy : 23; pl. 5, fig. 15.
1951*b* *Glandulina nipponica* Asano : 14, text-figs 71–72.
1959 *Glandulina laevigata* (d'Orbigny); Graham & Militante : 70; pl. 10, figs 29a, b.
1960 *Glandulina laevigata* (d'Orbigny); Chang : pl. 13, figs 8, 9.
1963 *Glandulina nipponica* Asano; Matsunga : pl. 33, fig. 7.

MATERIAL. 7 specimens. NB 9449, 9450.

VARIATION. Length 0·24–0·62 mm, breadth 0·14–0·37 mm.

REMARKS. Cushman & Ozawa (1930) reported that topotypes of *G. laevigata* were invariably biserial in the initial portion, not uniserial as originally figured by d'Orbigny. As this character

(Loeblich & Tappan 1964: C537) is critical to the diagnosis of the genus, our synonymy is restricted to records of specimens illustrated or described as initially biserial.

Distribution. *Fossil*: Miocene of the Vienna Basin (topotypes; Cushman & Ozawa 1930), Taiwan (Chang 1960) and Sumatra (Le Roy 1944); Late Tertiary (? Upper Miocene/Pliocene) of eastern Borneo and Japan (Le Roy 1941 and Matsunaga 1963, respectively); Pliocene of Japan (Asano 1951*b*) and Plio-Pleistocene of Java (Le Roy 1941*b*). *Recent*: The Philippines (Graham & Militante 1959) and Guam (Cushman 1933).

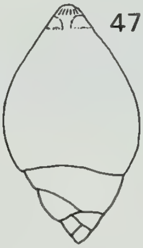


Fig. 47 *Glandulina laevigata* (d'Orbigny). P50258. Sample NB 9450. ×70.

Subfamily OOLININAE Loeblich & Tappan, 1961

Genus *OOLINA* d'Orbigny, 1839

Type-species: *Oolina laevigata* d'Orbigny, 1839.

Oolina hexagona (Williamson)

Pl. 4, fig. 2

1848 *Entosolenia squamosa* (Montagu) var. γ *hexagona* Williamson: 20; pl. 2, fig. 23.
1960 *Oolina hexagona* (Williamson) Barker: 120; pl. 58, fig. 33 (? 32) (after Brady 1884).

Material. 2 specimens. NB 9449, 9450.

Variation. Length 0·20–0·28 mm, greatest breadth 0·16–0·22 mm.

Range. Pliocene (Asano 1951*e*) to Recent.

Oolina squamosa (Montagu)

Pl. 4, fig. 1

1803 *Vermiculum squamosum* Montagu: 5; pl. 14, fig. 2.
1973 *Oolina squamosa* (Montagu) Haynes: 110; pl. 14, fig. 14; pl. 15, figs 4, 5.

Material. 8 specimens. NB 9450, 9452.

Variation. Length 0·20–0·43 mm, greatest breadth 0·17–0·34 mm.

Remarks. For a reinterpretation of this species see Haynes (1973: 110–111).

Range. Miocene (Le Roy 1964) to Recent.

Genus *FISSURINA* Reuss, 1850

Type-species: *Fissurina laevigata* Reuss, 1850.

Fissurina circularis Todd

Pl. 4, fig. 3

1954 *Fissurina circularis* Todd *in* Cushman, Todd & Post: 351; pl. 87, fig. 27.

Material. 4 specimens. NB 9449.

Variation. Length 0·24–0·27 mm, breadth 0·21–0·27 mm, thickness 0·13–0·15 mm.

Range. Uncertain; believed to be the first fossil record from the Indo–west Pacific.

Fissurina radiatomarginata (Parker & Jones)
Fig. 48

1865 *Lagena sulcata* Walker & Jacob var. *marginata* (Montagu) subvar. *radiato-marginata* Parker & Jones: 348, 355; pl. 18, figs 3a, b.
1954 *Fissurina radiato-marginata* (Parker & Jones) Cushman, Todd & Post: 351; pl. 87, fig. 29.

MATERIAL. 2 specimens. NB 9449.

DIMENSIONS. Length 0·30 mm, breadth 0·16 mm, thickness 0·09 mm.

RANGE. Pliocene (Yabe & Asano 1937, Le Roy 1964) to Recent.

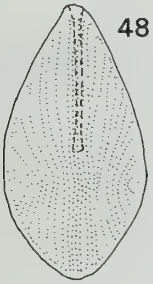


Fig. 48 *Fissurina radiatomarginata* (Parker & Jones). P50259. Sample NB 9449. ×125.

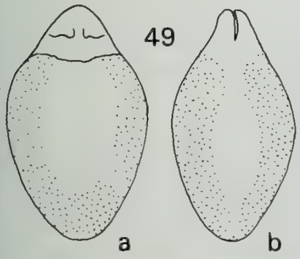
Fissurina spp.
Figs 49–51

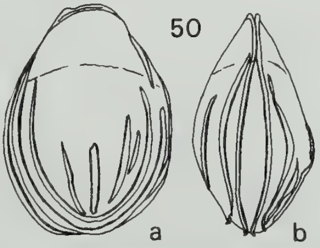
Species 1. Figs 49a, b.

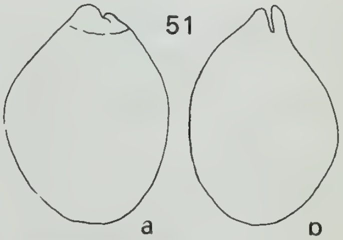
MATERIAL. 7 specimens. NB 9450, 9460.

VARIATION. Length 0·27–0·37 mm, greatest breadth 0·21–0·27 mm, thickness 0·18–0·23 mm.

REMARKS. A slightly flattened smooth test; wall transparent except for densely perforate areas forming a horseshoe-shaped opaque pattern on either side of the subacute periphery.







Figs 49a, b *Fissurina* sp. 1. P50260. Side and edge views. Sample NB 9450. ×90.
Figs 50a, b *Fissurina* sp. 2. P50261. Side and edge views. Sample NB 9450. ×140.
Figs 51a, b *Fissurina* sp. 3. P50262. Side and edge views. Sample NB 9450. ×80.

Species 2. Figs 50a, b.

MATERIAL. 5 specimens. NB 9449, 9450, 9452.

VARIATION. Length 0·22–0·25 mm, greatest breadth 0·17–0·20 mm, thickness 0·13–0·14 mm.

REMARKS. Test with 16–18 ribs of unequal length: some are confined to the basal region, some to the middle, while only the principal peripheral ribs extend over the whole length of the shell.

Species 3. Figs 51a, b.

Material. 7 specimens. NB 9450, 9452.

Variation. Length 0·22–0·39 mm, breadth 0·16–0·30 mm, thickness 0·16–0·27 mm.

Remarks. Test smooth, almost as thick as broad. There is little difference in the density of perforations over the body of the shell, except in the apertural region where it is transparent.

Family **BOLIVINITIDAE** Cushman, 1927

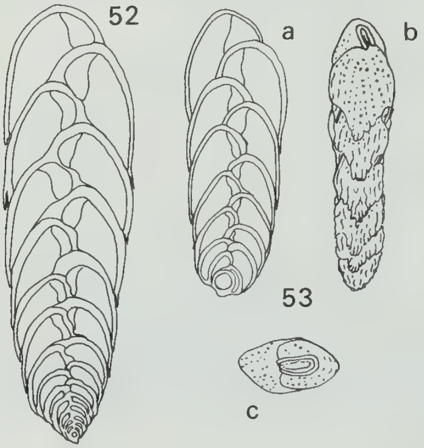
Genus ***BOLIVINA*** d'Orbigny, 1839

Type-species: *Bolivina plicata* d'Orbigny, 1839.

Bolivina sabahensis sp. nov.

Figs 52–53c; Pl. 4, fig. 4

Diagnosis. A moderately compressed *Bolivina* with a subovate periphery in apertural view. Sides of test sub-parallel, all but the last few chambers ornamented by irregularly developed longitudinal striae which cross and mask the early sutures.



Figs 52–53c *Bolivina sabahensis* sp. nov. 52, P50113. **Holotype** (microspheric form), side view in clearing medium. See also Pl. 4, fig. 4. 53a–c, P50114. Paratype (megalospheric form). Side view in clearing medium, edge and apertural views. Both from sample NB 9450. ×85.

Name. Described from Sabah, Malaysia.

Holotype. BM(NH) reg. no. P50113, from sample NB 9450.

Material. 41 specimens. NB 9447, 9450.

Description (Holotype: microspheric). Test biserial, calcareous, coarsely perforate, sides hardly tapering except at initial end. Ovate in apertural view with subacute peripheries; thickness virtually constant in edge view. Initial chamber pointed; chambers, 13 in each series, increasing regularly in size and becoming slightly inflated. Ornament of irregular longitudinal striae best developed in early part of the test; on later part restricted to basal portion of chambers where it tends to overlap the sutures. Depressed sutures only seen between last three pairs of chambers. Aperture elongate, sub-terminal, reaching base of apertural face.

Dimensions (Holotype). Length 0·67 mm, breadth 0·20 mm, thickness 0·13 mm.

Variation. Size range of paratypes:

	Microspheric (5 specimens)	*Megalospheric*
Length	0·42–0·67 mm	0·34–0·72 mm
Breadth	0·14–0·20 mm	0·12–0·20 mm
Thickness	0·10–0·15 mm	0·10–0·13 mm

The number of chambers (including the proloculus) varies between 19 and 27 in the microspheric and between 11 and 17 in the megalospheric form.

Remarks. The microspheric specimens are clearly distinguished by the pointed initial end; megalospheric forms are truncate initially (Fig. 53a). In both generations later sutures tend to become inclined at a greater angle than the earlier sutures. The tooth plate protrudes through the aperture and internally reaches the previous aperture. At low magnifications under the optical microscope the ornament is barely visible and the test appears glossy and highly perforate.

Our specimens have been compared with the following species of similar appearance.

Bolivina bilaensis Le Roy, from the Miocene of Sumatra.
Bolivina tikutoensis Nakamura, from the Pliocene of Taiwan.
Bolivina victoriana Cushman, from the Miocene of Australia.
Bolivina vadescens Cushman, from the Recent of Fiji.

None of them are thought by us to be conspecific. Our material usually differs in apertural aspect and in the number of chambers for a given size; furthermore, none of them appear to possess striate ornament although, as we have stated above, this is often difficult to see in *B. sabahensis*. Of the previously-described striate species of *Bolivina*, the widespread *B. striatula* Cushman is superficially similar but it has only a small number of regular costae on the early chambers and is very compressed in the later part. D. J. Belford has kindly compared our specimens with the many bolivinids in the Neogene of Papua–New Guinea (Belford 1966). He reports that although it is most similar to his own *Brizalina vescistriata* it is not as narrow and elongate and has less distinct striations.

See also Postscript, p. 106.

Genus *BRIZALINA* Costa, 1856

Type-species: *Brizalina aerariensis* Costa, 1856.

Brizalina amygdalaeformis (Brady) *iokiensis* (Asano)
Pl. 4, figs 5, 6

1938*b* *Loxostoma amygdalaeforme iokiense* Asano : 605; pl. 16, figs 3a, b.
1950*a* *Loxostoma amygdalaeforme iokiense* Asano; Asano : 10, text-fig. 41.
1964 *Loxostomum amygdalaeforme* (Brady) var. *iokiense* Asano; Le Roy : F33; pl. 2, figs 22, 23.

Material. 21 specimens. NB 9448, 9449, 9450, 9452.

Variation. Length 0·30 to more than 0·75 mm (broken specimen), breadth 0·20–0·28 mm, thickness 0·13–0·16 mm. Number of chambers: microspheric form up to 18; megalospheric form 11–15.

Remarks. This species is referred to *Brizalina* because it lacks the retral chamber processes ('basal chamber lobes' of Belford 1966) and crenulations of *Bolivina*. Moreover, the wall is radial in structure, not granular as in the genus *Loxostomum*.

B. amygdalaeformis iokiensis is characterized by numerous, strong, slightly sinuous, irregularly bifurcating costae; the aperture is subterminal, rarely terminal, with an internal toothplate, bordered by raised thickened lips which are continuations of one of the marginal costae.

Huang (1968) re-examined Nakamura's species *Bolivina formosana*. He concluded that the type-specimen was a juvenile and illustrated other adult, but broken specimens, from the Pliocene Wumeikeng Formation of Taiwan. Unfortunately his illustrations (1968 : pl. 3, figs 13, 14; pl. 8, figs 1–6; text-fig. 2) are poor and we cannot determine whether *B. formosana* is conspecific with our material or not, although it appears similar in size and shape. Since Nakamura's original figure (1937 : pl. 12, figs 2a, b) may have misled subsequent workers, it is possible that *Loxostomum amygdalaeforme* (Brady) *iokiense* Asano may be a junior synonym. However, as the latter is somewhat better known and has been well illustrated, we prefer to use this name for our specimens.

The raised border to the aperture (giving it a compressed appearance), plus strong costate ornament over the entire test, distinguish it from the Recent Philippines species *Bolivina amygdalaeformis* Brady.

See also Postscript, p. 106.

DISTRIBUTION. *Fossil*: Miocene–Pliocene of Okinawa (Le Roy 1964); Pliocene of Japan (Asano 1938*b*, 1950*a*) and possibly Taiwan (Nakamura 1937; Huang 1968). This subspecies does not appear to have been found in post-Pliocene deposits.

Genus ***RECTOBOLIVINA*** Cushman, 1927

Type-species: *Sagrina bifrons* Brady, 1881. Examination of the type specimens of *Sagrina bifrons* Brady in the British Museum (Natural History) confirms that both generations are biserial initially, later rectilinear and uniserial, with toothplates alternating at 180°. This is in agreement with the diagnosis of *Rectobolivina* by Loeblich & Tappan (1964 : C553).

Rectobolivina raphana (Parker & Jones)

Pl. 4, fig. 8

1865 *Uvigerina* (*Sagrina*) *raphanus* Parker & Jones : 364; pl. 18, figs 16a, b.
1884 *Sagrina raphanus* (Parker & Jones); Brady : 585; pl. 75, figs 21, 22, ? 23 only.
1913 *Siphogenerina raphanus* (Parker & Jones) Cushman : 108; pl. 46, figs 1–5.
1926 *Siphogenerina raphanus* (Parker & Jones); Cushman : 4; pl. 1, figs 1–4 (1, 2 after Parker & Jones).
1931 *Siphogenerina raphanus* (Parker & Jones); Hada : 134, text-figs 91a, b.
1942 *Siphogenerina raphana* (Parker & Jones); Cushman : 55; pl. 15, figs 6–9.
1949 *Siphogenerina raphana* (Parker & Jones); Said : 34; pl. 3, fig. 26.
1950*a* *Siphogenerina raphanus* (Parker & Jones); Asano : 14, text-figs 56, 57.
1954 *Siphogenerina raphana* (Parker & Jones); Cushman, Todd & Post : 356; pl. 88, figs 23, 24.
1956 *Siphogenerina raphanus* (Parker & Jones); Bhatia : 21; pl. 1, fig. 6d only.
1957 *Siphogenerina raphana* (Parker & Jones); Todd : 290 (table); pl. 89, figs 12a, b.
1959 *Siphogenerina raphanus* (Parker & Jones); Graham & Militante : 87; pl. 13, fig. 8.
1960 *Siphogenerina raphanus* (Parker & Jones); Barker : 156; pl. 75, figs 21, 22, ? 23 only (after Brady).
1962 *Siphogenerina raphanus* (Parker & Jones); Kuwano : text-fig. 8 (table); pl. 22, figs 5a, b.
1963 *Siphogenerina raphanus* (Parker & Jones); Matsunaga : pl. 42, figs 8a, b.
1964*a* *Siphogenerina raphanus* (Parker & Jones); Rocha & Ubaldo : 413; pl. 5, fig. 3.
1970 *Siphogenerina raphana* (Parker & Jones); Kim : 107 (table); pl. 1, fig. 13.

MATERIAL. 22 specimens. NB 9450.

VARIATION. Length not exceeding 1·2 mm, breadth up to 0·26 mm.

REMARKS. These specimens, which are all megalospheric, bear 12–14 ribs; the chamber shape varies but is usually clearly visible particularly in adult specimens. The initial portion of the shell is biserial. Toothplates in the rectilinear uniserial part alternate through 180°. These specimens are closely similar to the lectotype and paralectotypes (selected by Loeblich & Tappan 1964) which have been examined in a clearing medium and found not to include any completely uniserial form.

DISTRIBUTION. *Fossil*: ? Upper Miocene/Pliocene and Pliocene of Japan (Matsunaga 1963 and Asano 1950*a*, respectively). *Recent*: Widespread throughout the Indo-Pacific region in Recent sediments.

Rectobolivina raphana (Parker & Jones), var.

MATERIAL. 8 specimens. NB 9449.

VARIATION. Length 0·40–1·05 mm, breadth 0·11–0·24 mm. Number of biserial chambers up to 7, number of uniserial chambers 3–7, longitudinal ribs 7–13.

REMARKS. These specimens differ from *R. raphana* in having a more prominent biserial portion.

Rectobolivina striata (Schwager) var. ***curta*** (Cushman)

Pl. 4, fig. 9

1884 *Sagrina striata* (Schwager); Brady : 584; pl. 75, figs (? 25), 26.
1913 *Siphogenerina striata* (Schwager) Cushman : 107; pl. 47, figs 4a, b, 5.

1921 *Siphogenerina striata* (Schwager); Cushman : 280; pl. 56, fig. 5.
1926 *Siphogenerina striata* (Schwager) var. *curta* Cushman : 8; pl. 2, fig. 5.
1941 *Rectobolivina bifrons* (Brady) var. *striatula* (Cushman); Le Roy: 35; pl. 2, figs 7, 8 (*non Siphogenerina bifrons* (Brady) var. *striatula* Cushman, 1917).
1949 *Siphogenerina striata* (Schwager); Boomgaart : 121; pl. 9, fig. 2.
? 1957 *Siphogenerina* 3 (*S. striata* (Schwager)); Daleon & Samaniego : 48; pl. 1, fig. 52.
1960 *Siphogenerina striata* (Schwager) var. *curta* Cushman; Barker (*pars*) : 156; pl. 75, figs (? 25), 26 (after Brady).
1961 *Siphogenerina striata* (Schwager); Braga : 148; pl. 15, fig. 21.
1964 *Rectobolivina bifrons* (Brady) var. *striatula* (Cushman); Le Roy : F34; pl. 3, figs 5, 6.
1964 *Siphogenerina striata* (Schwager) var. *curta* Cushman; Rocha & Ubaldo : 93; pl. 8, figs 8, 9.

MATERIAL. 11 specimens. NB 9450.

VARIATION. Length 0·40–1·05 mm, breadth 0·11–0·24 mm. Number of biserial chambers usually 7, number of uniserial chambers 3–7, number of ribs 20–35.

REMARKS. Ribbing is variable: it may be strong and continuous over many chambers or weakly developed with breaks at the sutures. There is, however, no gradation to *R. raphana* (Parker & Jones) in our material. All the Togopi specimens are initially biserial with toothplates alternating at 180°, thus justifying the use of the generic name.

The record of Daleon & Samaniego (1957) is questioned owing to poor reproduction of the figure in our copy of their publication.

DISTRIBUTION. *Fossil*: ? Lower Miocene of Java (Boomgaart 1949), Late Tertiary (? Upper Miocene–Lower Pliocene) of eastern Borneo (Le Roy 1941), Neogene of Panay Island, Philippines (Daleon & Samaniego 1957), Miocene–? Pliocene of Okinawa (Le Roy 1964) and Holocene (2 m raised beach) of Timor (Rocha & Ubaldo 1964). *Recent*: North Pacific (Brady 1884, etc.) and Mozambique Coast (Braga 1961).

Family **BULIMINIDAE** Jones, 1875
Subfamily **PAVONININAE** Eimer & Fickert, 1899
Genus ***PAVONINA*** d'Orbigny, 1826

Type-species: *Pavonina flabelliformis* d'Orbigny, 1826.

Pavonina flabelliformis d'Orbigny
Pl. 4, figs 11a, b

1826 *Pavonina flabelliformis* d'Orbigny : 260; pl. 10, figs 10–12.

MATERIAL. 1 specimen. NB 9450.

DIMENSIONS. Length 0·45 mm, breadth 0·44 mm, thickness 0·10 mm.

REMARKS. A probably immature specimen with few chambers and a pointed initial end. The arrangement of the chambers in the initial portion is not known as it appeared opaque when viewed in clearing media. The apertural face is pustulate, bearing pores of various sizes. For further information on this genus see Cushman (1926 : 19–24), Parr (1933) and Hofker (1951*b*).

RANGE. We believe this to be the first fossil record from Indonesia (Parr 1933).

Genus ***CHRYSALIDINELLA*** Schubert, 1908

Type-species: *Chrysalidina dimorpha* Brady, 1881.

Chrysalidinella dimorpha (Brady)
Pl. 4, fig. 14

1881 *Chrysalidina dimorpha* Brady : 54.
1884 *Chrysalidina dimorpha* Brady; Brady : 388; pl. 46, figs 20, 21.

MATERIAL. 4 specimens. NB 9450 (? 9449).

VARIATION.

	Microspheric	*Megalospheric*
Length	0·70–0·94 mm	0·52–0·65 mm
Width	0·30–0·52 mm	0·31–0·34 mm

RANGE. Pliocene (Yabe & Asano 1937) to Recent.

Genus ***REUSSELLA*** Galloway, 1933

Type-species: *Verneuilina spinulosa* Reuss, 1850.

Reussella sp.

Pl. 4, fig. 13

MATERIAL. 6 specimens. NB 9449, 9450, 9452.

VARIATION. Length 0·28–0·44 mm, breadth 0·21–0·28 mm. Number of chambers 10–14.

REMARKS. Closely resembles *Fijiella* (*Reussella*) *simplex* (Cushman) in shape but possessing a toothplate and a single semilunar instead of a cribrate aperture. Our specimens may be compared with *Verneuilina spinulosa* Reuss (Brady 1884 : 384; pl. 47, figs 1a, b only), *Ruessella* sp. C (Todd & Post 1954 : 559; pl. 199, fig. 11) and *Reussella simplex* Cushman (Todd 1957 : pl. 89, figs 23a, b).

Family **UVIGERINIDAE** Haeckel, 1894

Genus ***SIPHOGENERINA*** Schlumberger *in* Milne-Edwards, 1882

Type-species: *Siphogenerina costata* Schlumberger, 1883.

Siphogenerina sp.

Pl. 4, fig. 7

MATERIAL. 3 specimens. NB 9450.

VARIATION. Length 0·50–0·60 mm, width (uniserial portion) 0·15–0·20 mm, (biserial portion) 0·17–0·21 mm. Number of chambers in uniserial and biserial portions respectively 2–3 and ? 8–10.

REMARKS. Examination in a clearing medium appeared to show toothplates set at 120° apart, thus suggesting *Siphogenerina* rather than *Rectobolivina*. The early part of the test is somewhat obscured by pyrite.

Genus ***SIPHOUVIGERINA*** Parr, 1950

Type-species: *Uvigerina porrecta* Brady var. *fimbriata* Sidebottom, 1918.

Siphouvigerina proboscidea (Schwager) var. ***vadescens*** (Cushman)

Pl. 4, fig. 10

1933*a* *Uvigerina proboscidea* Schwager var. *vadescens* Cushman : 85; pl. 8, figs 14, 15.
1942 *Uvigerina proboscidea* Schwager var. *vadescens* Cushman; Cushman : 50; pl. 14, figs 5–9.
1948 *Uvigerina proboscidea* Schwager var. *vadescens* Cushman; Todd *in* Cushman & McCulloch : 268; pl. 34, fig. 5.
1962 *Uvigerina proboscidea vadescens* Cushman; Kuwano : text-fig. 8 (table); pl. 24, fig. 9.
1964 *Uvigerina proboscidea vadescens* Cushman; Ishiwada : 41; pl. 5, fig. 78.
1964 *Uvigerina proboscidea* Schwager var. *vadescens* Cushman; Le Roy : F35; pl. 3, fig. 38.
1965 *Uvigerina vadescens* Cushman; Aoki : 57; pl. 7, figs 9, 10.

MATERIAL. 17 specimens. NB 9449, 9450, 9452, 9460.

VARIATION. Length 0·25–0·48 mm, breadth 0·15–0·18 mm.

REMARKS. This species has been transferred to *Siphouvigerina* since in many adult specimens the later chambers become biserial or even uniserial, and the simple toothplate is entirely devoid of a wing. Cushman differentiated his variety from Schwager's species by its smaller size, more slender form and elongate apertural neck. Examination of topotype specimens of *U. proboscidea* from Car Nicobar, identified by Dr M. S. Srinivasan and deposited in the British Museum (Natural History), has confirmed Cushman's varietal diagnosis.

In 1965, Aoki accorded specific rank to this variety without any explanation.

DISTRIBUTION. *Fossil*: Miocene–Pliocene of Okinawa (Le Roy 1964), Plio-Pleistocene of Japan (Aoki 1965). *Recent*: Guam (Cushman 1933*a*), Fiji (Cushman 1942), Japan (Kuwano 1962, Ishiwada 1964) and 'various tropical localities' (figured specimen locality not specified – Todd *in* Cushman & McCulloch 1948).

Family **DISCORBIDAE** Ehrenberg, 1838

Subfamily **DISCORBINAE** Ehrenberg, 1838

Genus ***DISCORBIS*** Lamarck, 1804

Type-species: *Discorbites vesicularis* Lamarck, 1804.

Discorbis cf. ***dimidiatus*** (Parker & Jones)

Pl. 4, fig. 12

cf. 1862 *Discorbina dimidiata* Parker & Jones: 201, text-fig. 32b.
cf. 1967 *Discorbis dimidiatus* (Parker & Jones); Hedley, Hurdle & Burdett: 33; pl. 1, fig. 4; pl. 10, figs 1–3; text-figs 28–43.

MATERIAL. 10 specimens. NB 9447, 9449.

VARIATION. Length 0·28–0·60 mm, breadth 0·21–0·25 mm, thickness 0·15–0·29 mm. Number of chambers in first whorl 5, in second 5–7 and in final whorl 4–7.

REMARKS. Hedley, Hurdle & Burdett (1967), in their extensive review of *Discorbina dimidiata* Parker & Jones, concluded that it was specifically distinct from the Eocene *Discorbites vesicularis* Lamarck. Furthermore, they considered the genus *Lamellodiscorbis* (type *D. dimidiata*) to be superfluous.

Our small number of immature poorly-preserved specimens are tentatively referred to *Discorbis dimidiatus*, based on the evidence of intraspecific variability illustrated by Hedley *et al.* from Australian and New Zealand Recent material.

Genus ***GAVELINOPSIS*** Hofker, 1951

Type-species: *Discorbina praegeri* Heron-Allen & Earland, 1913.

Gavelinopsis sp.

Pl. 4, figs 18a, b

MATERIAL. 3 complete and 8 broken specimens. NB 9447, 9449.

VARIATION. Length 0·22–0·27 mm, breadth 0·20–0·25 mm, thickness 0·09–0·14 mm. Number of chambers in first, second and final whorls 5–6, 6–8 and 6–7 respectively.

REMARKS. Placed in *Gavelinopsis* by virtue of its small umbilical plug (Loeblich & Tappan 1964: C578). It must be noted, however, that the validity of the genus is questioned by Haynes (1973: 161).

Our poorly-preserved trochospiral specimens with coarse perforations on the spiral side are similar to *Discorbina praegeri* Heron-Allen & Earland and, except for the presence of a plug, to *Discorbis laddi* Kleinpell.

Genus ***ROSALINA*** d'Orbigny, 1826

Type-species: *Rosalina globularis* d'Orbigny, 1826.

Rosalina bradyi (Cushman)

Pl. 4, figs 15, 16

1884 *Discorbina globularis* (d'Orbigny); Brady : 643; pl. 86, figs 8a–c only (*non Rosalina globularis* d'Orbigny, 1826).
1915 *Discorbina globularis* (d'Orbigny); Heron-Allen & Earland : 694; pl. 51, figs 36–39.
1915 *Discorbis globularis* (d'Orbigny) var. *bradyi* Cushman : 12; pl. 8, figs 1a–c.
1933*a* *Discorbis opima* Cushman : 88; pl. 9, figs 3a–c.
1933*a* *Discorbis micens* Cushman : 89; pl. 9, figs 5a–c.
1951*d* *Discopulvinulina bradyi* (Cushman) Asano : 4, text-figs 25, 26.
1954 *Discorbis globularis* (d'Orbigny); Kleinpell : 56; pl. 5, figs 1a–c.
1954 *Discorbis micens* Cushman; Cushman, Todd & Post : 358; pl. 89, figs 8, 9.
1954 *Discorbis opima* Cushman; Cushman, Todd & Post : 358; pl. 89, figs 10, 11.
1957 *Discorbis micens* Cushman; Todd : 290 (table); pl. 90, figs 7a–c.
1957 *Discorbis opima* Cushman; Todd : 290 (table); pl. 90, figs 11a–c.
1959 *Rosalina globularis* d'Orbigny; Graham & Militante : 97; pl. 14, figs 12a–c.
1960 *Rosalina bradyi* (Cushman) Barker : 178; pl. 86, figs 8a–c (after Brady).
1967 *Rosalina bradyi* (Cushman); Hedley, Hurdle & Burdett : 42; pl. 1, fig. 3; pl. 11, figs 2a–c; text-figs 50–55.
1968 *Rosalina bradyi* (Cushman); Albani : 109; pl. 9, figs 1, 2, 5, 6.
1970 *Rosalina bradyi* (Cushman); Matoba : 60; pl. 4, figs 8a–c.

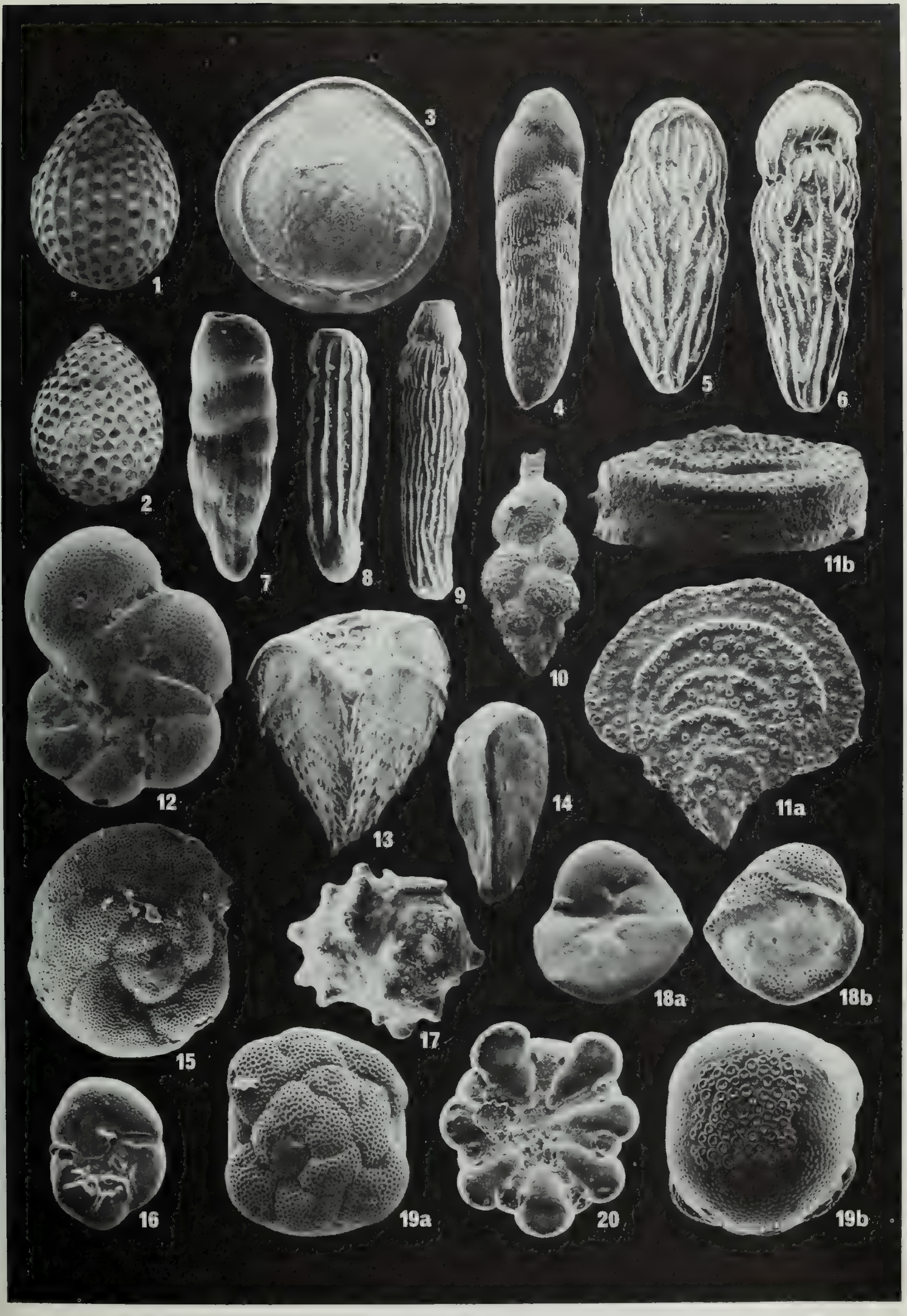
MATERIAL. 11 specimens. NB 9447, 9449.

VARIATION. Maximum diameter 0·25–0·55 mm, thickness 0·10–0·27 mm. Numbers of chambers in first whorl 5–7, in second 5–9 and in final whorl 4–5.

REMARKS. The taxonomic position and intraspecific variation of this species have been discussed in some detail by Hedley, Hurdle & Burdett (1967).

Plate 4 Scanning Electron Micrographs

Fig. 1 *Oolina squamosa* (Montagu). P50110. Side view. Sample NB 9452. ×100.
Fig. 2 *Oolina hexagona* (Williamson). P50111. Side view. Sample NB 9450. ×100.
Fig. 3 *Fissurina circularis* Todd. P50112. Side view. Sample NB 9449. ×150.
Fig. 4 *Bolivina sabahensis* sp. nov. P50113. Side view of **holotype** (microspheric form). Sample NB 9450. ×75. (See Fig. 52, p. 54.)
Figs 5, 6 *Brizalina amygdalaeformis* (Brady) *iokiensis* (Asano). P50115, P50116. Side views of megalospheric and microspheric forms. Sample NB 9450. ×75.
Fig. 7 *Siphogenerina* sp. P50117. Side view. Sample NB 9450. ×70.
Fig. 8 *Rectobolivina raphana* (Parker & Jones). P50118. Side view. Sample NB 9450. Approx. ×50.
Fig. 9 *Rectobolivina striata* (Schwager) var. *curta* (Cushman). P50119. Side view. Sample NB 9450. Approx. ×50.
Fig. 10 *Siphouvigerina proboscidea* (Schwager) var. *vadescens* (Cushman). P50120. Side view. Sample NB 9450. ×100.
Figs 11a, b *Pavonina flabelliformis* d'Orbigny. P50121. Side and apertural views. Sample NB 9450. ×100.
Fig. 12 *Discorbis* cf. *dimidiatus* (Parker & Jones). P50122. Ventral (umbilical) view. Sample NB 9449. ×75.
Fig. 13 *Reussella* sp. P50123. Side view. Sample NB 9449. ×100.
Fig. 14 *Chrysalidinella dimorpha* (Brady). P50124. Side view. Sample NB 9450. ×50.
Figs 15, 16 *Rosalina bradyi* (Cushman). P50125, P50126. Dorsal and ventral views. Sample NB 9447. Both specimens ×75.
Fig. 17 *Siphoninoides echinatus* (Brady). P50127. Side view. Sample NB 9450. ×100.
Figs 18a, b *Gavelinopsis* sp. P50128. Ventral and dorsal views. Sample NB 9447. ×100.
Figs 19a, b, 20 *Cymbaloporetta plana* (Cushman). Figs 19a, b, P50130, P50129. Dorsal and ventral side of '*Tretomphalus*'-form. Fig. 20, P50131. Ventral side of specimen without float-chamber. All specimens from sample NB 9449. ×75.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18a
18b
19a
19b
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DISTRIBUTION. *Fossil*: Upper Miocene/Lower Pliocene of Fiji (Kleinpell 1954); Pliocene of Japan (Asano 1951*d*). *Recent*: Recorded from Japan to New South Wales and New Zealand, and from the Kerimba Islands (Mozambique).

Subfamily **BAGGININAE** Cushman, 1927

Genus *CANCRIS* de Montfort, 1808

Type-species: *Nautilus auricula* Fichtel & Moll, 1798.

Cancris auriculus (Fichtel & Moll)

Pl. 5, fig. 10

1798 *Nautilus auricula* Fichtel & Moll var. α : 108; pl. 20, figs a–c; var. β : 110; pl. 20, figs d–f.
1921 *Pulvinulina auricula* (Fichtel & Moll) Cushman : 329; pl. 69, figs 3a–c.
1931 *Cancris auricula* (Fichtel & Moll) Hada : 139, text-figs 94a–c.
1939 *Cancris auricula* (Fichtel & Moll); Le Roy : 259; pl. 3, figs 1–3.
1941 *Cancris auriculus* (Fichtel & Moll); Le Roy : 41; pl. 2, figs 79–81.
1941*b* *Cancris auriculus* (Fichtel & Moll); Le Roy : 117; pl. 3, figs 7–9, 16–18.
1942 *Cancris auriculus* (Fichtel & Moll); Cushman & Todd : 74; pl. 18, figs 1–11.
1944 *Cancris auriculus* (Fichtel & Moll); Le Roy : 36; pl. 3, figs 4–9.
1949 *Cancris auriculus* (Fichtel & Moll); Said : 38; pl. 4, fig. 9.
1951*d* *Cancris auriculus* (Fichtel & Moll); Asano : 19, text-figs 144, 145.
1956 *Cancris auricula* (Fichtel & Moll); Bhatia : 23; pl. 5, figs 5a, b.
1959 *Cancris auriculus* (Fichtel & Moll); Graham & Militante : 91; pl. 13, figs 18a, b.
1960 *Cancris auriculus* (Fichtel & Moll); Chang ; pl. 14, figs 8a–c.
1963 *Cancris auriculus* (Fichtel & Moll); Matsunaga : pl. 47, figs 8a, b.
1964 *Cancris auriculus* (Fichtel & Moll); Le Roy : F39; pl. 6, figs 23, 24.
? 1964 *Cancris auriculus* (Fichtel & Moll); Carter : 84; pl. 5, figs 87–89.
1965 *Cancris auriculus* (Fichtel & Moll); Todd : 22; pl. 5, figs 5a–c.
1966 *Cancris auriculus* (Fichtel & Moll); Belford : 96; pl. 15, figs 1–5.
1968 *Cancris auriculus* (Fichtel & Moll); Antony : 97; pl. 7, figs 5a, b.
1971 *Cancris auricula* (Fichtel & Moll); Rao : 170 (table), text-fig. 52.
1974 *Cancris auriculus* (Fichtel & Moll); Lutze : 29; pl. 6, figs 108, 109.

MATERIAL 22 specimens. NB 9449, 9450, 9460.

VARIATION. Length 0·35–0·77 mm, breadth 0·23–0·58 mm, thickness 0·15–0·24 mm. Number of chambers 7–8.

REMARKS. For comments on this species see Cushman & Todd (1942), who figured topotypes and whose illustrations (pl. 18, figs 4a–c) have formed the basis for subsequent identifications; Haynes (1973 : 147) compares and contrasts it with the closely-related *Cancris oblongus* Williamson.

The specific name has been variously construed as *auriculus*, *auricula* and *auriculatus*, the last-mentioned name being modified without reason by de Montfort (1808 : 267) from Fichtel & Moll's original name. The gender of *Cancris* is discussed by MacFadyen & Kenny (1934 : 180) who concluded that it should be taken as being masculine.

DISTRIBUTION. *Fossil*: Miocene of Sumatra (Le Roy 1939, 1944) and Taiwan (Chang 1960); late Tertiary (? Upper Miocene–Lower Pliocene) of east Borneo (Le Roy 1941); Pliocene of Japan (Asano 1951*d*, Matsunaga 1963), Okinawa (Le Roy 1964), New Guinea (Belford 1966) and Victoria, Australia (? Carter 1964); Plio-Pleistocene of Java (Le Roy 1941*b*). The types are from the Pliocene of Italy (Fichtel & Moll 1798, Cushman & Todd 1942) (= var. *α*) and the Recent of the Mediterranean (= var. *β*). *Recent*: This species appears to be common throughout the Indo-Pacific at the present day.

Cancris sp.

Pl. 5, fig. 5

MATERIAL. 9 specimens. NB 9447, 9449.

VARIATION. Length 0·20–0·35 mm, breadth 0·18–0·26 mm, thickness 0·15–0·21 mm. Number of chambers 7–13, with 5–6 in the final whorl.

REMARKS. A small species with lobulate periphery. It may have affinities with *Baggina gibba* Cushman & Todd (1944*a* : 104; pl. 16, figs 8a–c) and the *Discorbina rugosa* d'Orbigny of Egger (1893 : 191; pl. 15, figs 1–3). The umbilical area is open in larger specimens, closed in smaller, usually with a lip. The former features are common to both *Baggina* and *Valvulineria*, while the apertural lip suggests *Cancris*.

Family **GLABRATELLIDAE** Loeblich & Tappan, 1964

Genus *SCHACKOINELLA* Weinhandl, 1958

Type-species: *Schackoinella sarmatica* Weinhandl, 1958.

'Schackoinella' globosa (Millett)[2]

Pl. 5, figs 11, 12a, b; Pl. 10, fig. 6

1903*a* *Discorbina imperatoria* (d'Orbigny) var. *globosa* Millett : 701; pl. 7, figs 6a, b.
1915 *Rotalia erinacea* Heron-Allen & Earland : 720; pl. 53, figs 23–26.
1963 '*Eponides*' *globosus* (Millett) Ujiié : 233; pl. 1, figs 27a–c only.
1967 *Pararotalia minuta* (Takayanagi); Matoba : 256; pl. 27, figs 5a, b (*non Rotalia* ? *minuta* Takayanagi, 1955).
1967 *Pararotalia minuta* (Takayanagi) var. Matoba : 256; pl. 27, figs 6a, b.
1968 *Pararotalia* cf. *imperatoria* (d'Orbigny) var. *globosa* (Millett); Chiji & Lopez : 109; pl. 12, figs 5a–c.
1971 *Schackoinella sarmatica* Weinhandl; Haman & Christensen : 44, text-figs 1–3 (*non S. sarmatica* Weinhandl 1958).

MATERIAL. 43 specimens. NB 9447, 9449, 9450.

VARIATION. Maximum diameter 0·14–0·25 mm, thickness 0·07–0·15 mm. Number of chambers in last whorl 5–6.

REMARKS. This small, calcareous, monolamellar, perforate, almost planoconvex species bears one spine on each of the later-formed chambers; the coil is a low trochospire. The umbilical area is infilled thus obscuring the aperture, but it is probably umbilical extra-umbilical.

Heron-Allen & Earland (1915) found that their material from Kerimba was conspecific with Millett's (1903*a*) types. Unfortunately, Millett's types have not been isolated in the collections of the British Museum (Natural History) and therefore it has only been possible to compare the Togopi specimens with *R. erinacea* Heron-Allen & Earland. We consider them to be conspecific. These authors' new name, however, is not now necessary: at the time (1915) they referred the species to *Rotalia* and thus rightly considered the name *globosa* was preoccupied by *Nonionina globosa* von Hagenow, a Cretaceous species from Germany, which was also, they believed, a *Rotalia*. As the name *globosa* is a secondary homonym it can be used for our form, as the two species are certainly not congeneric (see I.C.Z.N. code, articles 57 and 59c). Millett's name, furthermore, is acceptable as a taxon in the species-group as it is published with the term 'variety' before 1961 and therefore is to be interpreted as denoting subspecific rank (articles 45d(i), 45e(i)). Article 46 states that at the same time it is available as a specific name.

Specimens of *Schackoinella sarmatica* identified by Haman & Christensen from the Yellow Sea have been studied by us under the scanning electron microscope. They are probably juveniles of the present species. It is considered better to place this species in *Schackoinella*, as defined by Loeblich & Tappan (1964 : C591), than in *Pararotalia*, the apertural characteristics of which are very different. Recently the suprageneric position of *Schackoinella* within the Rotaliina has been disputed by El-Naggar (1971), who would include it within the Globigerinacea.

We believe that *S. globosa* may have been confused with *Rotalia murrayi* Heron-Allen & Earland (1915 : 721; pl. 53, figs 27–34) by some earlier workers. At Kerimba, the type area for both species, they occur together in abundance only at stations 7 and 8. In size they are closely similar, but '*Rotalia*' *murrayi* is clearly separated by the coarse rugosity of the test which in places is projected into 'acute papillae' as described by Heron-Allen & Earland.

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[2] See Postscript, p. 106; species transferred to *Murrayinella* Farias, 1977 (? Rotaliidae).

DISTRIBUTION. *Fossil*: Plio-Pleistocene (Matoba 1967) and Holocene (Ujiié 1963) of Japan. *Recent*: Malay Archipelago (Millett 1903*a*), Kerimba Archipelago, East Africa (Heron-Allen & Earland 1915), Tanabe Bay, Japan (Chiji & Lopez 1968) and the Yellow Sea (Haman & Christensen 1971).

Family **SIPHONINIDAE** Cushman, 1927

Genus ***SIPHONINOIDES*** Cushman, 1927

Type-species: *Planorbulina echinata* Brady, 1879.

Siphoninoides echinatus (Brady)

Pl. 4, fig. 17

1879 *Planorbulina echinata* Brady : 283; pl. 8, figs 31a–c.
1884 *Truncatulina echinata* (Brady) Brady : 670; pl. 96, figs 9–14.
1915 *Truncatulina echinata* (Brady); Heron-Allen & Earland : 711; pl. 53, fig. 1.
1915 *Siphonina echinata* (Brady) Cushman : 42; pl. 18, figs 1–4 (after Brady); text-figs 46, 47.
? 1927 *Siphoninoides echinata* (Brady) Cushman : 13; pl. 4, figs ? 7a, b only.
1949 *Siphoninoides echinata* (Brady); Said : 38; pl. 4, fig. 6.
1954 *Siphoninoides echinata* (Brady); Cushman, Todd & Post : 361; pl. 89, figs 31, 32.
1957 *Siphoninoides echinata* (Brady); Todd : 290 (table); pl. 91, figs 7a, b.
1959 *Siphoninoides echinatus* (Brady); Graham & Militante : 102; pl. 16, figs 2a, b.
1960 *Siphoninoides echinata* (Brady); Barker : 198; pl. 96, figs 9–14 (after Brady).
1965 *Siphoninoides echinatus* (Brady); Todd : 23; pl. 15, figs 5, 6.
1969 *Siphoninoides echinatus* (Brady); Resig : 84; pl. 5, fig. 5.

MATERIAL. 8 specimens. NB 9447, 9450.

VARIATION. Maximum diameter 0·21–0·32 mm.

REMARKS. Hofker (1970 : 32; pl. 33) discusses *Siphoninoides* from the Caribbean and tentatively assigns it to the Glabratellidae. Unfortunately we are not in a position to verify his findings due to lack of material.

Western Pacific material from the 'Challenger' and Millett collections shows that the strength and number of the spines and prominence of the sutures in the last whorl are variable in this species.

The correct ending for the specific name is *echinatus*. According to MacFadyen & Kenny (1934) all genera ending in *-oides* should be taken as being masculine.

DISTRIBUTION. *Fossil*: Pleistocene, Ewa Borehole, Hawaii (Resig 1969). There is a further possible fossil record from the Miocene of Victoria, Australia. *Recent*: Common in the western Pacific islands (excluding Japan). Said (1949) records it from the Red Sea.

Family **EPISTOMARIIDAE** Hofker, 1954

Genus ***EPISTOMAROIDES*** Uchio, 1952

Type-species: *Discorbina polystomelloides* Parker & Jones, 1865.

Epistomaroides polystomelloides (Parker & Jones)

Pl. 5, figs 1, 2; Pl. 10, fig. 17

1865 *Discorbina polystomelloides* Parker & Jones : 421; pl. 19, figs 8a–c.
1884 *Discorbina polystomelloides* Parker & Jones; Brady : 652; pl. 91, figs 1a–c.
1915 *Discorbina polystomelloides* Parker & Jones; Heron-Allen & Earland : 698; pl. 52, figs 19–23.
1927 *Rotalia polystomelloides* (Parker & Jones) Hofker : 35; pl. 16, figs 1–6.
1938 (?) *Epistomaria polystomelloides* (Parker & Jones); Howchin & Parr : 303; pl. 17, figs (? 5, ? 6), 7, 11–13.
1952 *Epistomaroides polystomelloides* (Parker & Jones) Uchio : 158; pl. 7, figs 1a–3c.

1954 *Epistomaroides polystomelloides* (Parker & Jones); Cushman, Todd & Post: 360; pl. 89, fig. 26.
? 1954 *Epistomaria polystomelloides* (Parker & Jones); Crespin: 45; pl. 6, figs 8a, b.
1957 *Epistomaroides polystomelloides* (Parker & Jones); Todd: 290 (table); pl. 93, figs 10a–c.
1959 *Epistomaroides rimosus* (Parker & Jones); Graham & Militante: 94; pl. 14, figs 4a–c (*non Discorbina rimosa* Parker & Jones, 1862).
1960 *Epistomaroides polystomelloides* (Parker & Jones); Barker: 188; pl. 91, figs 1a–c (after Brady).
1965 *Epistomaroides polystomelloides* (Parker & Jones); Le Calvez: 191; pl. 13, fig. 2.
1965 *Epistomaroides polystomelloides* (Parker & Jones); Todd: 25; pl. 10, figs 5, 6a–c.
1969 *Epistomaroides polystomelloides* (Parker & Jones); Resig: 59; pl. 5, figs 10a, b.

MATERIAL. 23 specimens. NB 9447, 9449, 9450.

VARIATION. Maximum diameter 0·41–1·25 mm, thickness 0·12–0·35 mm. Number of chambers in first whorl 5–6, second whorl 5–9, final whorl 7–10.

REMARKS. Loeblich & Tappan (1964) rediagnosed the genera *Epistomaroides* and *Epistomaria* and selected lectotypes for their respective type-species *Discorbina polystomelloides* Parker & Jones and *Discorbina rimosa* Parker & Jones. *D. rimosa*, according to them, is restricted to the Eocene of Europe. All the Recent Indo-Pacific specimens labelled *D. rimosa* in the Parker Collection (British Museum (Natural History)) are without exception clearly referable to *D. polystomelloides*, as are Parker & Jones' Recent records of *D. rimosa* from the Australian coral reefs (*in* Carpenter 1862) and India (1865); similarly, Graham & Militante's specimen (1959: pl. 14, figs 4a–c) from the Philippines is almost certainly *D. polystomelloides*.

The paralectotypes of *Epistomaroides polystomelloides* (BM(NH) no. ZF 3602) show that there is a considerable range of variation within the species from a coarsely roughened test (see Parker & Jones' type-figure) to one where surface ornament is reduced and the septal bridges are clearly defined (see specimens illustrated by Heron-Allen & Earland 1915).

DISTRIBUTION. *Fossil*: Pliocene of South Australia (Howchin & Parr 1938, Crespin 1954); Pleistocene of Hawaii (Resig 1969). *Recent*: Widespread in the western Pacific from Japan to Australia, with two records from east Africa (Comores, Le Calvez 1965, and Kerimba Archipelagos, Heron-Allen & Earland 1915).

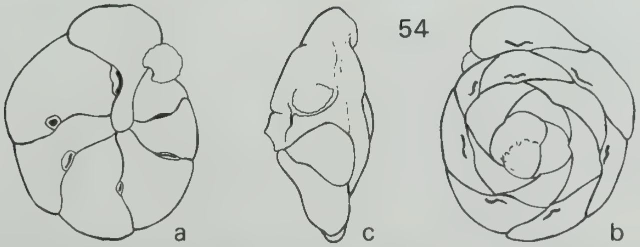
Genus *PSEUDOEPONIDES* Uchio *in* Kawai *et al.*, 1950

Type-species: *Pseudoeponides japonica* Uchio, 1950.

Pseudoeponides japonicus Uchio

Figs 54a–c

1950 *Pseudoeponides japonica* Uchio *in* Kawai *et al.*: 190, text-fig. 16.
1950 *Epistomaria* (*Epistomariella*) *miurensis* Kuwano: 315; figs 3a–c, 10.
1951 *Pseudoeponides japonicus* Uchio; Uchio: 38; pl. 3, figs 1a–c.
1951*d* *Pseudoeponides japonicus* Uchio; Asano: 19, text-figs 138–140.
1963 *Pseudoeponides japonica* Uchio; Matsunaga: pl. 45, fig. 7.
1964 *Pseudoeponides japonicus* Uchio; Le Roy: F39; pl. 9, figs 20–22.
1967 *Pseudoeponides japonicus* Uchio; Matoba: 256; pl. 26, figs 20a–c.



Figs 54a–c *Pseudoeponides japonicus* Uchio. P50263. Ventral, dorsal and peripheral views. Sample NB 9449. ×90.

Material. 5 specimens. NB 9447, 9449.

Variation. Maximum diameter 0·26–0·35 mm, thickness 0·16–0·23 mm.

Remarks. The Togopi specimens agree closely with the type and most subsequent figures except that the supplementary sutural apertural slits on the ventral side tend to be much less conspicuous and less highly curved.

Distribution. ? Upper Miocene/Lower Pliocene of Japan (Matsunaga 1963) and Okinawa (Le Roy 1964); Pliocene (Kuwano 1950, Uchio 1950, 1951, Asano 1951*d*) and Plio-Pleistocene of Japan (Matoba 1967). The species does not appear to have been found living today.

Family **ROTALIIDAE** Ehrenberg, 1839
Subfamily **ROTALIINAE** Ehrenberg, 1839
Genus ***AMMONIA*** Brünnich, 1772

Type-species: *Nautilus beccarii* Linné, 1758.

Ammonia annectens (Parker & Jones)
Pl. 5, fig. 9

1865 *Rotalia beccarii* (Linné) var. *annectens* Parker & Jones: 422; pl. 19, figs 11a–c.
1904 *Rotalia annectens* Parker & Jones; Millett: 505; pl. 10, figs 6a–c.
1940 *Streblus annectens* (Parker & Jones) Ishizaki: 58; pl. 3, figs 12a, b, 13a, b.
1956 *Streblus annectens* (Parker & Jones); Bhatia: 22; pl. 3, figs 1, 2.
1961 *Rotalia annectens* Parker & Jones; Huang: 87; pl. 4, figs 10, 11.
1964 *Streblus annectens* (Parker & Jones); Bhatia & Bhalla: 79; pl. 2, figs 1a–c.
1964*b* *Streblus annectens* (Parker & Jones); Rocha & Ubaldo: 417; pl. 4, figs 3a–c.
1964 *Ammonia annectens* (Parker & Jones) Huang: 50; pl. 2, figs 3a–c; pl. 3, figs 1, 2; text-fig. 3.

Material. 145 specimens. NB 9448, 9449, 9450, 9452, 9454, 9456/7, 9460.

Variation.	*Microspheric form*	*Megalospheric form*
Maximum diameter	1·00–1·61 mm	0·59–1·25 mm
Thickness	0·50–0·85 mm	0·40–0·65 mm
Number of chambers in first whorl	5–6	4–7
Number of chambers in second whorl	7–8	8–12
Number of chambers in third whorl	7–9	9–16
Number of chambers in final whorl	15–22	7–17

Plate 5 Scanning Electron Micrographs

Figs 1, 2 *Epistomaroides polystomelloides* (Parker & Jones). P50132, P50133. Dorsal (spiral) and apertural views. Sample NB 9450. Both specimens ×50.

Fig. 3 *Pararotalia calcar* (d'Orbigny). P50134. Ventral view of ornate specimen akin to *Calcarina nicobarensis* Schwager. Sample NB 9449. ×60.

Fig. 4 *Asterorotalia pulchella* (d'Orbigny). P50135. Ventral view. Sample NB 9452. ×60.

Fig. 5 *Cancris* sp. P50136. Ventral view. Sample NB 9447. ×75.

Figs 6a–c *Ammonia togopiensis* sp. nov. P50137. Apertural, ventral and dorsal views. **Holotype,** sample NB 9449. ×30.

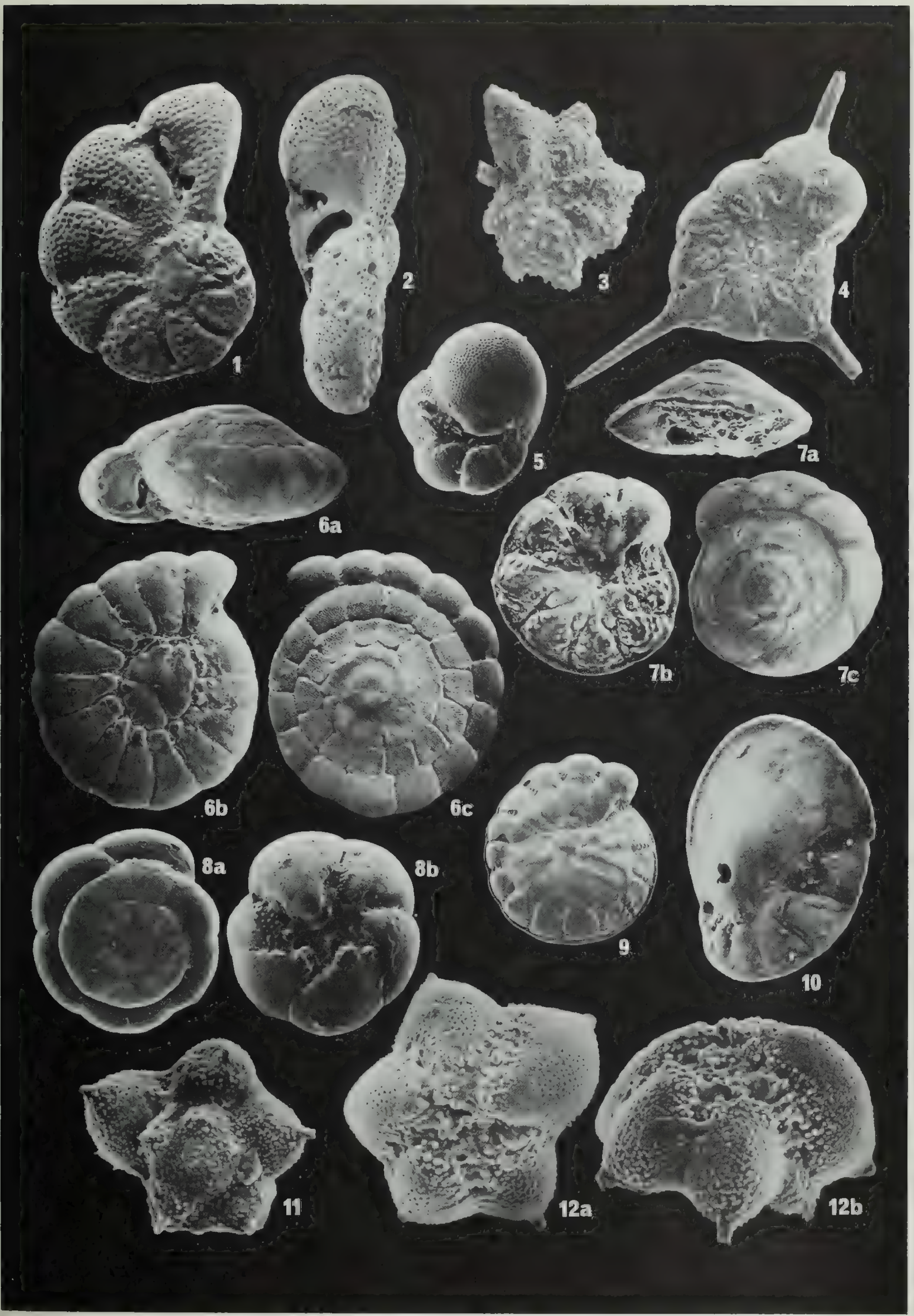
Figs 7a–c *Asterorotalia inspinosa* Huang. P50138. Apertural, ventral and dorsal views. Sample NB 9452. ×60.

Figs 8a, b *Ammonia beccarii* (Linné) var. *tepida* (Cushman). P50139. Dorsal and ventral views. Sample NB 9450. ×100.

Fig. 9 *Ammonia annectens* (Parker & Jones). P50140. Ventral view. Sample NB 9449. ×30.

Fig. 10 *Cancris auriculus* (Fichtel & Moll). P50141. Ventral view. Sample NB 9450. ×75.

Figs 11, 12a, b '*Schackoinella*' *globosa* (Millett). Fig. 11, P50142. Dorsal view. Sample NB 9447. Figs 12a, b, P50143. Ventral and oblique views. Sample NB 9450. All ×200.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REMARKS. Our specimens compare favourably with the type-figure of Parker & Jones 1865; the external trace of the toothplate clearly distinguishes it from *Streblus yabei* Ishizaki and *Rotalia beccarii* (Linné). The size, prominence and dissection of the umbilical plug, together with the development of the toothplate (protoforamen of Hofker, 1968) are its most striking features.

Examination of the Togopi material and of specimens from Hong Kong in the Parker Collection (BM(NH) no. 1894:4:3:1468) confirms Bhatia's observation (1956: 22) that in *A. annectens* there are two openings on the apertural face: a primary cameral aperture and beneath the umbilical portion of the chamber a toothplate foramen (see Hofker 1968) connected both to that of the previous chamber and to the protoforamen of the previous suture. As, however, the latter is not a true cameral aperture this species conforms to the diagnosis of *Ammonia* given by Loeblich & Tappan (1964: C607) and thus the use of the genus *Rotalidium* stipulated by Hofker (1968: 28) is unnecessary.

DISTRIBUTION. *Fossil*: Pliocene (Huang 1964) and Pleistocene (Huang 1964, Ishizaki 1940) of Taiwan. *Recent*: Hong Kong and Fiji (Parker & Jones 1865), Malay Archipelago (Millett 1904), Singapore (Ishizaki 1940), Penghu Is. (Huang 1961) and various Indian localities (Bhatia 1956, Bhatia & Bhalla 1964, Rocha & Ubaldo 1964*b*).

Ammonia beccarii (Linné) var. ***tepida*** (Cushman)
Pl. 5, figs 8a, b

1926*a* *Rotalia beccarii* (Linnaeus) var. *tepida* Cushman: 79; pl. 1.
1937 *Rotalia hozanensis* Nakamura: 141; pl. 12, figs 4a–c.
1954 *Rotalia* cf. *R. beccarii* var. *tepida* Cushman; Cushman, Todd & Post: 360; pl. 89, fig. 22.
1957 *Streblus beccarii* (Linné) var. *tepida* (Cushman) Todd: 290 (table); pl. 9, figs 5a–c.
1963 *Strebulus beccarii* (Linné) var. *tepida* (Cushman); Chiji: 65; pl. 7, figs 5a–6b, 8a, b (misspelling).
? 1963 *Ammonia* cf. *beccarii* (Linné) *tepida* (Cushman) Ujiié: pl. 2, figs 7a–c.
1964 *Streblus beccarii tepida* (Cushman); Le Roy: F38; pl. 4, figs 16, 17.
1964 *Ammonia hozanensis* (Nakamura) Huang: 53; pl. 1, figs 4a–c.
1965 *Streblus beccarii tepida* (Cushman); Todd: 29; pl. 6, figs 1a–c.
1967 *Ammonia beccarii tepida* (Cushman); Konda: 33 (table); pl. 4, figs 9a, b.
1968 *Ammonia beccarii* (Linné) var. *tepida* (Cushman); Chiji & Lopez: 104; pl. 12, figs 3a–4b.
1968 *Ammonia beccarii tepida* (Cushman); Chiji: 58 (table); pl. 3, figs 4a, b.
1968 *Ammonia hozanensis* (Nakamura); Huang: 90; pl. 5, figs 1–3.
1971 *Discorbis tepida* (Cushman) Seibold: 44; pl. 5, figs 4–6; pl. 6, figs 1–3; text-fig. 1.

Plate 6 Scanning Electron Micrographs

Figs 1, 2 *Pseudorotalia schroeteriana* (Parker & Jones). Apertural views. Fig. 1, P50144. Conical megalospheric specimen. Sample NB 9460. Fig. 2, P50145. 'Outgrown' adult megalospheric test. Sample NB 9449. Both specimens ×35.

Figs 3–5 *Pseudorotalia catilliformis* (Thalman). Fig. 3, P50146. Ventral view of megalospheric form. Sample NB 9454. Fig. 4, P50148. Ventral view of microspheric form. Sample NB 9452. Fig. 5, P50147. Dorsal view of microspheric form. Sample NB 9454. All specimens ×20.

Figs 6a–8b *Pseudorotalia indopacifica* (Thalmann). Figs 6a, b, P50149. Microspheric form, apertural and ventral views. Sample NB 9460. Fig. 7, P50150. Megalospheric form, apertural view. Sample NB 9449. Figs 8a, b, P50151. Megalospheric form, dorsal and ventral views. Sample NB 9460. All specimens ×25.

Figs 9a, b *Cellanthus hailei* sp. nov. P50152. Apertural and side views. **Holotype,** sample NB 9452. ×25.

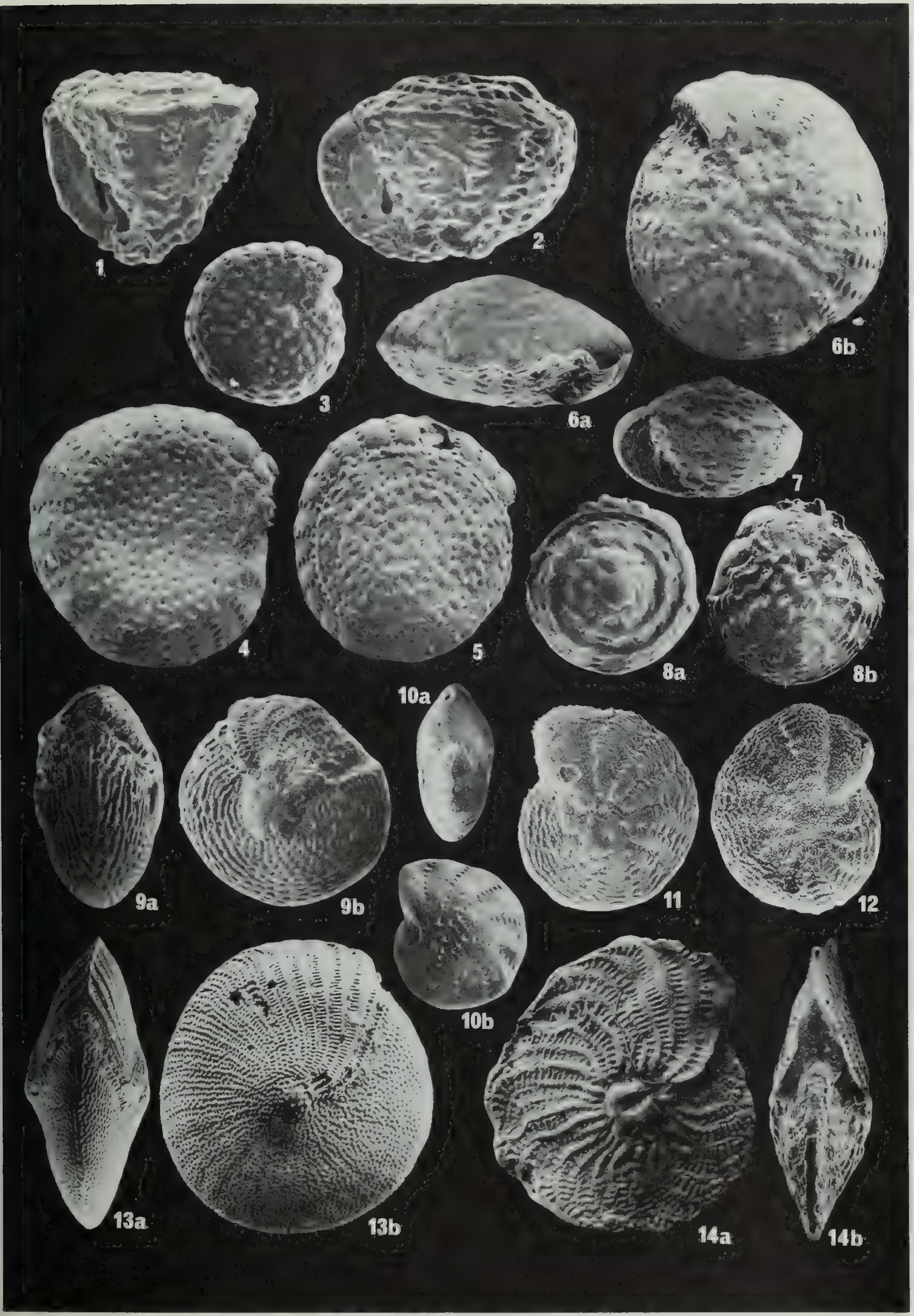
Figs 10a, b *Cribrononion tikutoensis* (Nakamura). P50153. Apertural and side views. Sample NB 9452. ×60.

Fig. 11 *Parrellina hispidula* (Cushman). P50154. Side view. Sample NB 9449. ×60.

Fig. 12 *Cribrononion reticulosus* (Cushman). P50155. Side view. Sample NB 9449. ×60.

Figs 13a, b *Cellanthus adelaidensis* (Howchin & Parr). P50156. Apertural and side views. Sample NB 9449. ×25.

Figs 14a, b *Elphidium* cf. *fax barbarense* Nicol. P50157. Side and apertural views. Sample NB 9449. ×30.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14b

MATERIAL. 35 specimens. NB 9446, 9447, 9450.

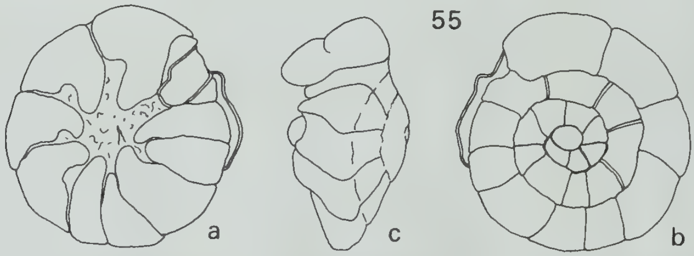
VARIATION. Maximum diameter 0·09–0·35 mm, thickness 0·09–0·20 mm. Number of chambers in last whorl 5–6.

REMARKS. In the Togopi samples this variety of the cosmopolitan species *Ammonia beccarii* shows varying degrees of chamber inflation in the final whorl. The earlier sutures, however, are limbate and flush. The umbilical depression is usually somewhat infilled with secondary material but is not plugged.

We have examined topotypic material housed in the BM(NH) from San Juan Harbour, Puerto Rico and consider ours to fall well within the range of variation found there. *Rotalia hozanensis* Nakamura is clearly a junior synonym as suggested by Huang (1968 : 90).

Schnitker (1974) studied cloned cultures of several North American 'species' of *Ammonia*, including *A. tepida* (Cushman), and concluded that only *A. beccarii* (Linné) was a valid taxon. For the present we follow his suggestion that the various 'ecophenotypes' should be recognized on an informal basis as varieties, while at the same time noting the conflicting findings of Seibold (1971), who on studying the internal structure of three members of the *A. beccarii* 'group' from south-west India concluded that only *R. beccarii* var. *sabrina* Shupack was a true *Ammonia*. *R. beccarii* var. *tepida* she placed in *Discorbis*, while *R. pauciloculata* Phleger & Parker was regarded as a species of *Pseudoeponides*. Clearly some further clarification of this problem is necessary.

DISTRIBUTION. *Fossil*: Pliocene of Taiwan (Nakamura 1937, Huang 1968) and Okinawa (Le Roy 1964), Pleistocene of Japan (Chiji 1963, Konda 1967) and Taiwan (Huang 1964) and Holocene of Japan (Ujiié 1963). *Recent*: Widespread in the tropical waters of the Indo-Pacific.



Figs 55a–c *Ammonia takanabensis* (Ishizaki). P50264. Ventral, dorsal and peripheral views. Sample NB 9447. × 115.

Ammonia takanabensis (Ishizaki)
Figs 55a–c

1948 *Streblus takanabensis* Ishizaki : 57; pl. 1, figs 5a–c.
1948 *Streblus nakamurai* Ishizaki : 62; pl. 1, figs 4a–c.
1950 *Rotalia maruhasii* Kuwano : 314, text-figs 2a–c.
1951*d* *Rotalia takanabensis* (Ishizaki) Asano : 16, text-figs 124–126.
? 1960 *Streblus* sp. cf. *S. takanabensis* Ishizaki ; Chang : pl. 14, figs ? 10a–c only.
1964 *Rotalia takanabensis* (Ishizaki); Kikuchi : pl. 5, figs 5, 6.
1964 *Streblus takanabensis* Ishizaki; Ishiwada : 14, 15 (table); pl. 6, figs 93a, b.
1964 *Ammonia takanabensis* (Ishizaki) Huang : 56; pl. 1, figs 2a–c.
1967 *Ammonia takanabensis* (Ishizaki); Matoba : 251; pl. 27, figs 3a–c.
1970 *Ammonia takanabensis* (Ishizaki); Kim : 108 (table); pl. 2, figs 4a–c.

MATERIAL. 9 specimens. NB 9447.

VARIATION. Maximum diameter 0·20–0·30 mm, thickness 0·12–0·16 mm. Number of chambers in last whorl 7–9.

Distribution. *Fossil*: Pliocene (Huang 1964) and possibly Miocene (Chang 1960) of Taiwan; Pliocene (Ishizaki 1948, Kuwano 1950, Asano 1951*d*) and Pleistocene (Matoba 1967, Kikuchi 1964) of Japan. *Recent*: Japan (Ishiwada 1964), Yellow Sea, west Korea (Kim 1970).

Ammonia togopiensis sp. nov.

Pl. 5, figs 6a–c; Pl. 10, figs 4, 5

1975 *Ammonia ikebei* (Inoue & Nakaseko); Billman & Kartaadipura : 306; pl. 1, figs 2a, b (*non Rotalia ikebei* Inoue & Nakaseko 1951).

Diagnosis. A large inflated trochoid species of *Ammonia* with rounded peripheries. Sutures of strongly convex dorsal side straight and incised. Ventral surface slightly to strongly convex, umbilical area infilled by large raised fissured plug. Chambers usually smooth and coarsely perforate.

Name. Described from the Togopi Formation.

Holotype. BM(NH) reg. no. P50137, from NB 9449.

Material. 40 specimens. NB 9446, 9447, 9449, 9450, 9452, 9456/7, 9460.

Description (Holotype: microspheric). Test calcareous, coarsely perforate, trochoid; periphery lobulate in side view, rounded in edge view. Slightly convex ventral surface showing 15 chambers in the last whorl and deeply fissured sutures lined by very faint bands or beads of hyaline shell material. Chambers slightly inflated, their umbilical ends bearing a non-perforate hyaline flap covering a space which is not in connection with the chamber by an aperture. Umbilical area infilled by a raised imperforate fissured plug. Dorsal surface strongly convex, early chambers obscured by thickening of the basal wall; later, sutures become depressed, radiate and straight giving a characteristic almost square shape to the chambers. In the final whorl chambers become quite inflated. Apertural face flat, confined to the ventral side. Aperture, an areal opening with lip and constriction.

Dimensions (Holotype). Maximum diameter 1·48 mm, thickness 0·75 mm, diameter of plug 0·50 × 0·40 mm, height of apertural face 0·35 mm.

Variation. Size range of paratypes:

	Microspheric	*Megalospheric*
Maximum diameter	0·90–1·75 mm	0·30–0·90 mm
Thickness	0·68–1·00 mm	0·30–0·53 mm
Plug diameter	up to 0·80 mm	up to 0·63 mm

The number of whorls varies from 4 to 8 in the microspheric, and between 2 and 3½ in the megalospheric form. Up to 19 chambers have been recorded in the last whorl of the microspheric form, while 10–13 chambers have been counted in the megalospheric form.

The megalospheric form is always biconvex, while the microspheric form varies between nearly planoconvex and biconvex dependent on the development of the plug (compare Pl. 5, fig. 6a and Pl. 10, fig. 4); in addition, some beading may be developed on the spiral sutures of the former generation. Other variables common to both generations are the prominence of the toothplate (very slight in the holotype), situated a quarter of the distance along the chamber from the plug, and the dissection of the plug which may be fissured around its edge or strongly dissected into pluglets.

Remarks. The only previous record of this species is under the name of *Ammonia ikebei* (Inoue & Nakaseko) from the Kutei Basin, offshore eastern Kalimantan (Borneo). There Billman & Kartaadipura (1975) use it as a Plio-Pleistocene zone fossil. However, their *A. ikebei* Zone, the top of which is placed at the highest stratigraphic occurrence of the nominate species, contains only rare planktonic foraminifera; calcareous nannoplankton are entirely absent. This age assignment is thus based solely on stratigraphic position. Material of this species kindly supplied by Billman from Kerindingan Well no. 1 shows that it occurs also in the preceding *Asanoina* Zone, which they date as Pliocene on nannoplankton.

Billman & Kartaadipura (1975 : pl. 1, figs 2a, b) figure a typical megalospheric form of our new species. However, their identification as *R. ikebei*, an obscure Miocene form from Japan subsequently stated by Asano (1951*d*: 15) to be 'an aberrant form' of *Rotalia nipponica* Asano, is unsatisfactory. Inoue & Nakaseko (1951 : text-figs 4a–c) show a much smaller form with curved instead of straight sutures on the dorsal side, many fewer chambers and a relatively smaller non-dissected plug on the ventral side.

DISTRIBUTION. Pliocene and Pleistocene of the Kutei Basin, eastern Borneo. The species does not appear to be living today.

Genus *ASTEROROTALIA* Hofker, 1951

Type-species: *Rotalina* (*Calcarina*) *pulchella* d'Orbigny *in* de la Sagra, 1839.

Asterorotalia pulchella (d'Orbigny)

Figs 56a–59c; Pl. 5, fig. 4

1839 *Rotalina* (*Calcarina*) *pulchella* d'Orbigny : 80; pl. 5, figs 16–18.
1884 *Rotalia pulchella* (d'Orbigny) Brady : 710; pl. 115, figs 8a, b.
1899 *Rotalia pulchella* (d'Orbigny); Flint : 332; pl. 76, fig. 3.
1927 *Rotalia pulchella* (d'Orbigny); Hofker : 37; pl. 16, figs 7–10.
1933 *Rotalia trispinosa* Thalmann : 249; pl. 12, figs 1a–c (= Indo-Pacific forms).
1933 *Rotalia cubana* Thalmann : 249; pl. 12, figs 2a–3b (= Cuban forms).
1937 *Rotalia trispinosa* Thalmann; Yabe & Asano : 103; pl. 18, fig. 11.
1951*d* *Rotalia trispinosa* Thalmann; Asano : 17, text-fig. 127.
1951*b* *Asterorotalia pulchella* (d'Orbigny) Hofker : 505, figs 343, 344.
1956 *Rotalia trispinosa* Thalmann; Marks : 43; pl. 25, figs 45a–f.
1958 *Asterorotalia pulchella* (d'Orbigny); Reiss & Merling : pl. 2, figs 2, 3; pl. 5, figs 12, 13.
1958 *Rotalia pulchella* (d'Orbigny); Ganapati & Satyavati : 104; pl. 5, figs 120, 121.
1960 *Asterorotalia trispinosa* (Thalmann); Barker : 238; pl. 115, figs 8a, b (after Brady).
1964 *Asterorotalia trispinosa* (Thalmann); Bhatia & Bhalla : 80; pl. 1, figs 10a, b.
1964 *Asterorotalia trispinosa* (Thalmann); Le Roy : F39; pl. 6, figs 18, 19.
1964 *Asterorotalia trispinosa* (Thalmann); Huang : 60; pl. 2, figs 10a, b; pl. 3, fig. 9.

Plate 7 Scanning Electron Micrographs

Figs 1, 2a, b *Cellanthus craticulatus* (Fichtel & Moll). Fig. 1, P50158. Side view of microspheric form. Figs 2a, b, P50159. Side and apertural views of megalospheric form. Both specimens from sample NB 9452. ×15.

Figs 3a, b *Cellanthus biperforatus* sp. nov. P50160. Apertural and side views. **Holotype,** sample NB 9452. ×25. (See Fig. 61, p. 84.)

Figs 4a, b *Cribroelphidium dentense* sp. nov. P50161. Apertural and side views. **Holotype,** sample NB 9452. ×60.

Figs 5–7 *Elphidiella indopacifica* Germeraad. Fig. 5, P50162. Side view of microspheric form. Figs 6, 7, P50163, P50164. Megalospheric specimens, side and apertural views. All from sample NB 9447. ×30.

Figs 8, 9 *Calcarina hispida* Brady. P50165, P50166. Ventral views. Sample NB 9450. ×30.

Fig. 10 *Gypsina globula* (Reuss). P50167. Side view. Sample NB 9452. ×20.

Fig. 11 *Poroeponides cribrorepandus* Asano & Uchio. P50168. Ventral view. Sample NB 9450. ×60.

Fig. 12 *Poroeponides lateralis* (Terquem). P50169. Ventral view. Sample NB 9450. ×60.

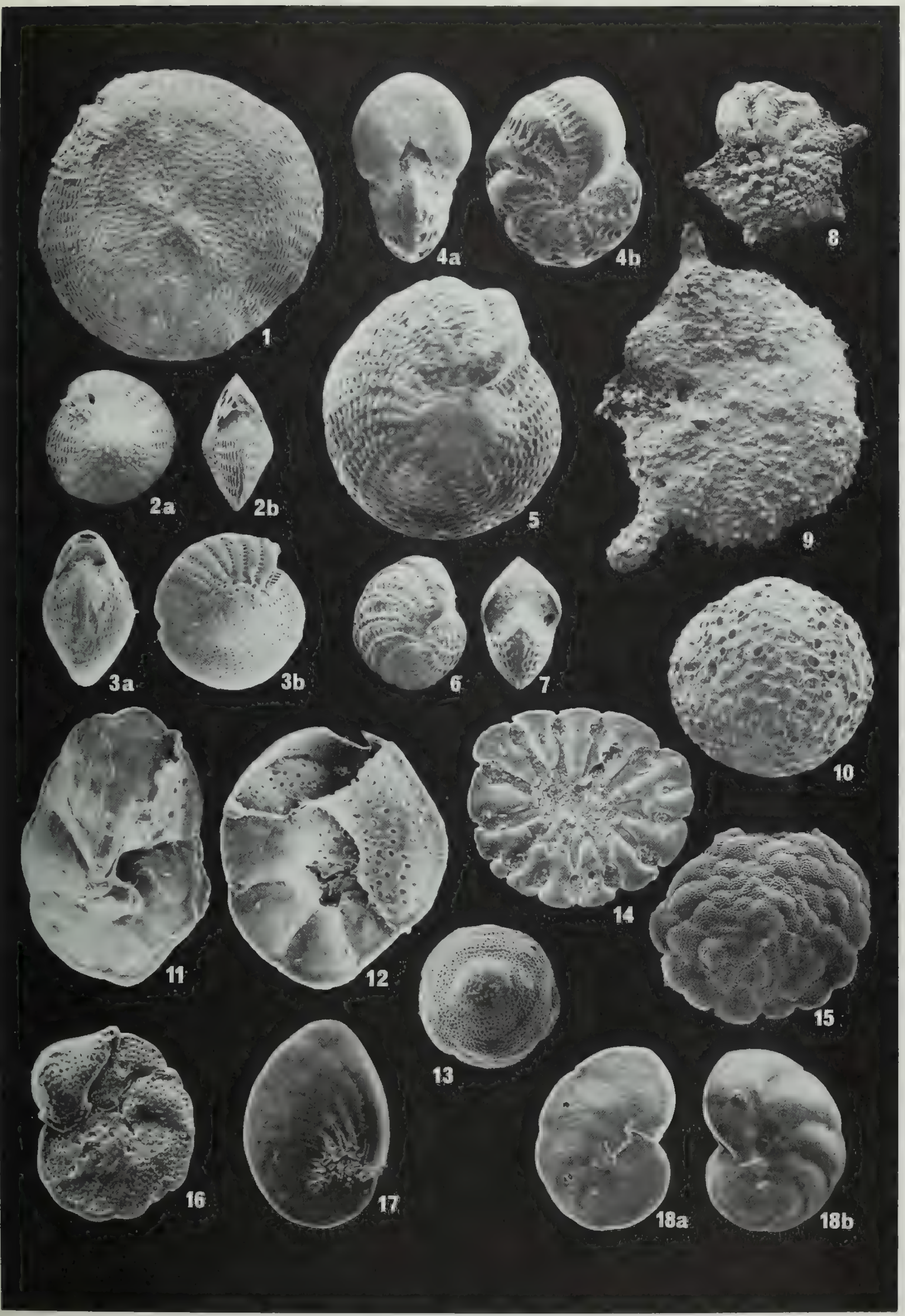
Fig. 13 *Cymbaloporetta squammosa* (d'Orbigny). P50170. Dorsal view. Sample NB 9449. ×45.

Figs 14, 15 *Cymbaloporetta bradyi* (Cushman). Fig. 14, P50171. Ventral view. Sample NB 9449. Fig. 15, P50172. Dorsal view. Sample NB 9450. Both specimens ×45.

Fig. 16 *Caribeanella ogiensis* (Matsunaga). P50173. Dorsal view. Sample NB 9450. ×60. (See Fig. 64, p. 101.)

Fig. 17 *Florilus asanoi* nom. nov. P50174. Side view. Sample NB 9452. ×80. (See Fig. 70, p. 104.)

Figs 18a, b *Hanzawaia nipponica* Asano. P50175. Dorsal (spiral) and ventral views. Sample NB 9450. ×100.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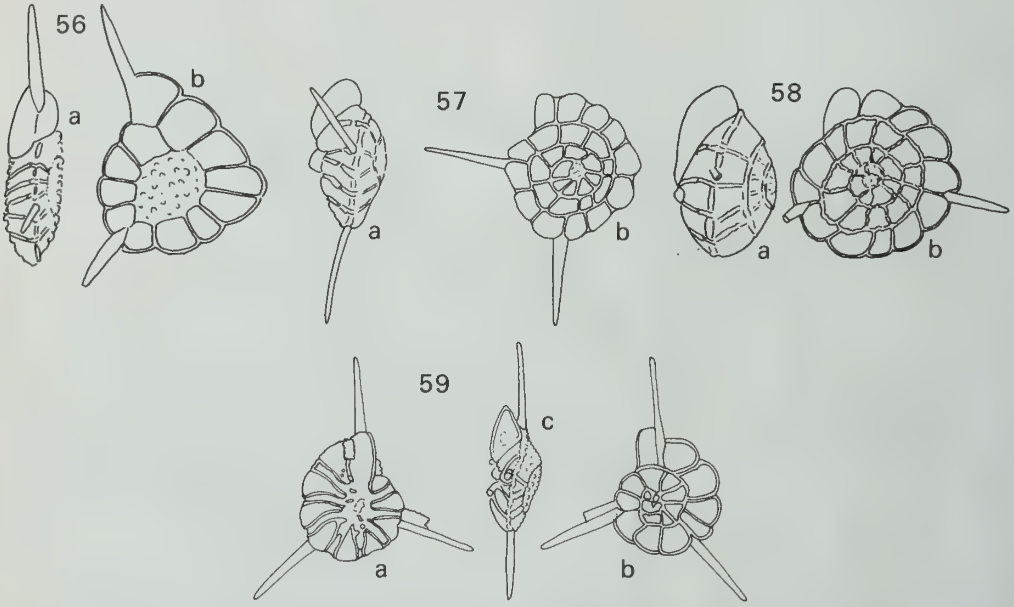
1968 *Asterorotalia trispinosa* (Thalmann); Bhalla : 382; pl. 2, figs 1a, b.
1968 *Asterorotalia pulchella* (d'Orbigny); Hofker : 27; pl. 8, figs 8–10; pl. 9, figs 1–7.
1971 *Asterorotalia pulchella* (d'Orbigny); Huang : 82, text-fig. 4D.

MATERIAL. About 500 specimens. NB 9448, 9449, 9450, 9452, 9453, 9454, 9455, 9456/7, 9460.

VARIATION. Diameter 0·21 × 0·16–0·97 × 0·68 mm (excluding spines), thickness 0·11–0·30 mm.



Figs 56a–59c *Asterorotalia pulchella* (d'Orbigny). 56–58, showing variation in shape as seen in Togopi sample NB 9449. P50265–P50267. Apertural and dorsal views. 56, 57, ×35; 58, ×40. 59a–c, ZF3826. Ventral, dorsal and apertural views. Recent, Dry Harbour, Jamaica. ×35.

Plate 8

Figs 1–10. Light microscopy
Figs 11–17. Scanning Electron Micrographs

Fig. 1 *Amphistegina* cf. *lessonii* d'Orbigny. P50176. Side view. Sample NB 9452. ×30.

Fig. 2 *Amphistegina* cf. *wanneriana* Fischer. P50177. Side view. Sample NB 9450. ×30.

Fig. 3 *Lagena clavata* (d'Orbigny). P50178. Side view. Sample NB 9449. ×100.

Fig. 4 *Lagena gracillima* (Seguenza). P50179. Side view. Sample NB 9449. ×50.

Fig. 5 *Lagena elongata* (Ehrenberg). P50180. Side view. Sample NB 9449. ×50.

Fig. 6 *Marginopora* cf. *vertebralis* de Blainville. P50181. Side view. Sample NB 9449. ×30.

Fig. 7 *Sigmoidella elegantissima* (Parker & Jones). P50182. Side view. Sample NB 9450. ×40.

Fig. 8 *Peneroplis planatus* (Fichtel & Moll) var. *annulata* nov. P50184. Side view. Sample NB 9452. ×15.

Figs 9, 10 *Heterostegina* sp. Fig. 9, P50185. Split specimen showing early part of the test. Sample NB 9452. ×15. Fig. 10, P50186. External view. Sample NB 9452. ×10.

Fig. 11 *Alveolinella quoyi* (d'Orbigny). P50187. Detail of part of apertural face. Sample NB 9452. Scale = 100 μm.

Fig. 12 *Globigerina quinqueloba* Natland. P50188. Oblique ventral view of broken specimen. Sample NB 9447. ×175.

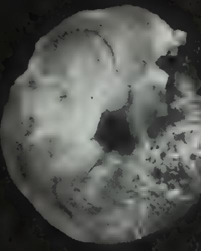
Fig. 13 *Globigerinita glutinata* (Egger). P50189. Oblique peripheral view of broken specimen. Sample NB 9449. ×200.

Fig. 14 *Globigerina bulloides* d'Orbigny. P50190. Oblique ventral view. Sample NB 9450. ×175.

Fig. 15 *Globigerinoides ruber* (d'Orbigny). P50191. Dorsal view. Sample NB 9449. ×100.

Fig. 16 *Globigerinoides sacculifer* (Brady). P50192. Oblique ventral view. Sample NB 9460. ×150.

Fig. 17 *Hastigerina siphonifera* (d'Orbigny). P50193. Oblique side view. Sample NB 9460. ×125.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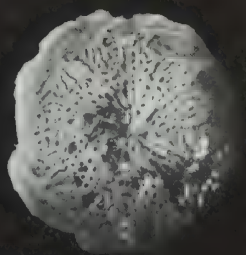
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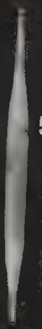
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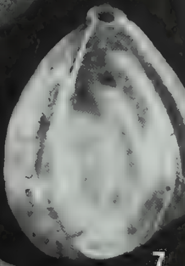
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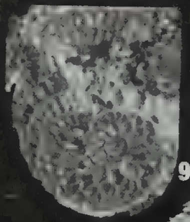
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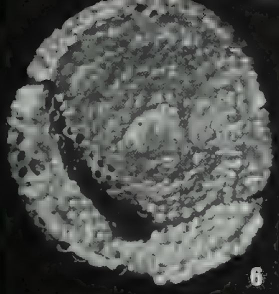
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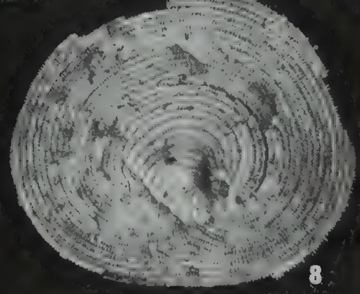
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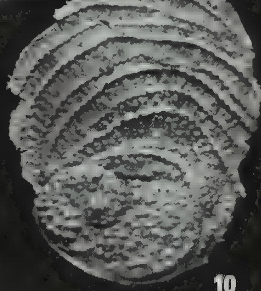
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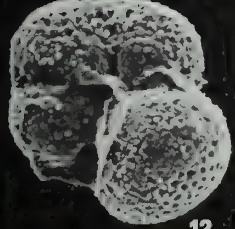
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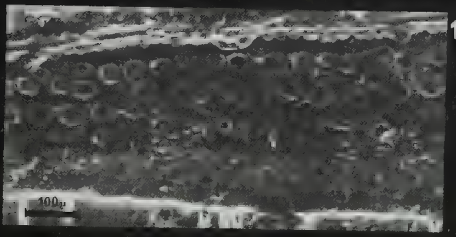

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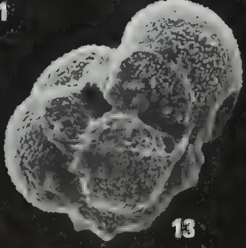
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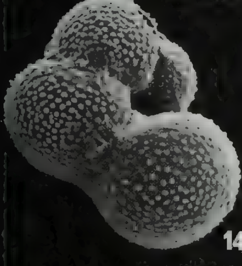
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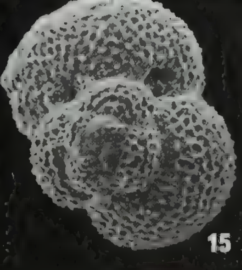
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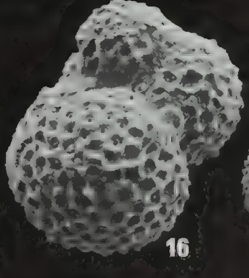
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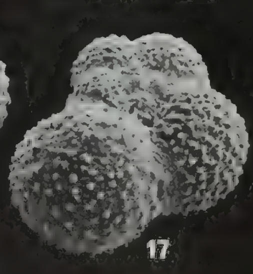
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REMARKS. The species occurs in all but the highest samples in the Togopi Formation and is most common in the middle of the succession. In the two lowermost samples (NB 9456/7, 9455) it is rare, poorly preserved and weakly ornamented, but from NB 9454 upwards *A. pulchella* becomes plentiful and the ornament (bars and beads) on the dorsal surface varies from very sparse to heavy on both chambers and sutures. The test is triangular to subcircular in side view and lenticular to semiglobular in apertural view. The specimens become more inflated higher in the succession and in NB 9449 a grading series is seen between lenticular and semiglobular forms (Figs 56a–58b). In NB 9448, only semiglobular forms occur. This intraspecific variation appears to be greater than is usually observed in Recent sediments from the Malay Archipelago, but there is no evidence in our samples of the evolutionary lineage (*A. inspinosa*→*A. pulchella*) postulated by Huang (1971), although it would be expected in rocks of this age. At Togopi, *Asterorotalia inspinosa* (see below) occurs in the same samples as *A. pulchella*.

There is a problem concerning the relationship between the Indo-Pacific and the Caribbean form, called by Thalmann *Rotalia cubana*. The only published record of this species from the Caribbean area appears to be that of d'Orbigny (1839) from Cuba. However, specimens in the Heron-Allen & Earland collection in the BM(NH), labelled Dry Harbour, north Jamaica (Figs 59a–c) seem, in our opinion, identical to many from the Togopi samples and there is, therefore, no reason to continue the use of different specific names for specimens from the two areas.

DISTRIBUTION. *Fossil*: Miocene of Okinawa (Le Roy 1964) and Japan (Asano 1951*d*); Upper Miocene/Lower Pliocene of Java (Yabe & Asano 1937); Pleistocene of Taiwan (Huang 1964, 1971) and Java (Marks 1956). *Recent*: Appears to be confined in our area to Indonesia and the coasts of India.

Asterorotalia inspinosa Huang

Pl. 5, figs 7a–c; Pl. 10, fig. 3

1963 *Rotalia nipponica* Asano; Matsunaga: pl. 45, figs 9a–c (*non R. nipponica* Asano 1936).
1964 *Ammonia nipponica* (Asano) Huang: 54; pl. 2, figs 1a–c.
1971 *Asterorotalia inspinosa* Huang: 83; pl. 1, figs 1a–5c; text-fig. 4A.

MATERIAL. 295 specimens. NB 9449, 9450, 9452, 9460.

VARIATION.	*Microspheric forms* (two specimens)	*Megalospheric forms*
Maximum diameter	0·64 mm	0·40–0·92 mm
Thickness	0·38 mm	0·20–0·48 mm
Number of whorls	4	3–4
Number of chambers in first whorl	7	5
Number of chambers in second whorl	7	8–9
Number of chambers in third whorl	10	9–11
Number of chambers in fourth whorl	11	11

REMARKS. Although lacking spines this species is retained in *Asterorotalia* since it has sutural plates on the ventral side.

In the Togopi specimens the beading on either side of the ventral sutures varies in prominence and density. The umbilical plug may be pronounced (for example in many specimens of sample NB 9450) or partially or completely covered (see Pl. 5, fig. 7b), its presence being only discovered by dissection or thin-sectioning. The cameral aperture is interiomarginal with lips; the plates of the labial apertures are much shorter than in the type-species.

DISTRIBUTION. Pliocene of Japan (Matsunaga 1963); late Miocene to late Pliocene of Taiwan (Huang 1964, 1971).

Genus ***PARAROTALIA*** Le Calvez, 1949

Type-species: *Rotalia inermis* Terquem, 1882.

Pararotalia calcar (d'Orbigny)

Pl. 5, fig. 3

1826 *Calcarina calcar* d'Orbigny : 276, no. 1; modèle 34.
1865*a* *Calcarina calcar* d'Orbigny; Parker, Jones & Brady : 24; pl. 3, fig. 87 (after d'Orbigny's model).
1866 *Calcarina nicobarensis* Schwager : 261; pl. 7, fig. 3.
1884 *Rotalia calcar* (d'Orbigny) Brady : 709; pl. 108, figs 3a–c only.
1893 *Rotalia calcar* (d'Orbigny); Egger : 423; pl. 19, figs 1–3.
1915 *Rotalia calcar* (d'Orbigny); Cushman : 69; pl. 28, figs 2a–c; pl. 29, figs 2a–c.
1921 *Rotalia calcar* (d'Orbigny); Cushman : 350; pl. 71, figs 3a, b.
1927 *Rotalia calcar* (d'Orbigny); Hofker : 37; pl. 17, figs 1–13.
1934 *Rotalia calcar* (d'Orbigny) ?; Caudri : 146; pl. 5, figs 7–9.
1941*a* *Rotalia calcar* (d'Orbigny); Le Roy : 84; pl. 7, figs 1–3.
1946 *Calcarina calcar* d'Orbigny; Germeraad : 70; pl. 4, fig. 1.
1946 *Calcarina umbilicata* Germeraad : 71; pl. 4, figs 2–5.
1954 *Rotalia calcar* (d'Orbigny); Kleinpell : 61; pl. 7, figs 5, 6.
1954 *Rotalia calcar* (d'Orbigny); Todd & Post : 560; pl. 202, figs 1a–c; pl. 203, figs 2, 3a, b.
1958 *Rotalia calcar* (d'Orbigny); Sethulekshmi Amma : 71; pl. 3, figs 113a, b.
1959 '*Rotalia*' *calcar* (d'Orbigny); Graham & Militante : 99; pl. 15, figs 2–3c.
1960 *Calcarina calcar* d'Orbigny; Barker : 222; pl. 108, figs 3a–c only (after Brady).
1964 *Calcarina calcar* d'Orbigny; Rocha & Ubaldo : 153; pl. 19, figs 5–7.
1965 *Calcarina calcar* d'Orbigny; Le Calvez : 191; pl. 13, fig. 1.
1965 *Calcarina calcar* d'Orbigny; Jell, Maxwell & McKellar : 277; pl. 44, figs 5a, b.
1970 *Pararotalia calcar* (d'Orbigny) Hofker : 55; pl. 41, figs 1–5; pl. 46, fig. 1.

MATERIAL. 26 specimens. NB 9447, 9449, 9450.

VARIATION. Maximum diameter 0·33–0·90 mm, thickness 0·17–0·20 mm.

REMARKS. These specimens are placed in *Pararotalia* as they have laterally elongated chambers, a plugged umbilicus and an interiomarginal and curved intercameral aperture. Ornament is variable and consists of pustules, particularly over the umbilical area, hyaline ridges along the chambers and hispid spines.

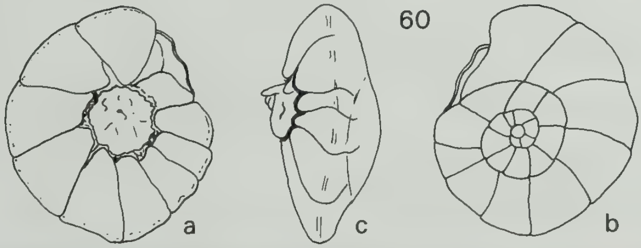
We have examined numerous Recent specimens attributed to *Calcarina calcar* d'Orbigny, including topotypic material from Madagascar, and conclude that the Togopi specimens fall within the range of variation of this species.

DISTRIBUTION. *Fossil*: Miocene of Fiji (Kleinpell 1954) and of Soemba Is., Indonesia (Caudri 1934), Neogene of Kar Nicobar, Indian Ocean (Schwager 1866), 'Young-Neogene' of Ceram Is., Indonesia (Germeraad 1946), post-Miocene of Bikini (Todd & Post 1954), Late Tertiary (? Pliocene) of Siberoet Is., Indonesia (Le Roy 1941*a*) and a sub-Recent raised beach in northernTimor (Rocha & Ubaldo 1964). *Recent*: Widespread in the Indian Ocean and in the East Indies and west Pacific Islands from Borneo to northern Australia. We know of no records from Japan.

Pararotalia cf. *nipponica* (Asano)

Figs 60a–c

cf. 1936 *Rotalia nipponica* Asano : 614; pl. 31, figs 2a–c.
cf. 1937 *Rotalia taiwanica* Nakamura : 141; pl. 12, figs 6a–c.
cf. 1951*d* *Rotalia ozawai* Asano : 15, text-figs 115–117.



Figs 60a–c *Pararotalia* cf. *nipponica* (Asano). P50268. Ventral, dorsal and peripheral views. Sample NB 9447. ×100.

MATERIAL. 24 specimens. NB 9446, 9447.

VARIATION. Maximum diameter 0·18–0·29 mm, thickness 0·13–0·21 mm. Number of chambers in last whorl 7–10.

REMARKS. A number of authors (e.g. Ujiié 1966, Bhalla 1972) have considered the possibility that *Rotalia nipponica*, *R. taiwanica* and *R. ozawai* may be conspecific.

R. nipponica is much larger than *R. taiwanica* (the types are twice the size), but Ujiié and Bhalla state the only other differences appear to be that the latter has a more lobulate periphery and smaller number of chambers. *R. ozawai* is similar in size to *R. taiwanica* and differs only in possessing small peripheral spiny projections. Furthermore, these two are often found together in Recent (e.g. Graham & Militante 1959) and fossil (e.g. Huang 1964) sediments. All three have a strong umbilical plug and belong to the genus *Pararotalia*. As all our material is small and of the *P. taiwanica* type we are not able to study variation and therefore can only concur tentatively with the thesis that *P. nipponica* is the only valid taxon.

DISTRIBUTION. *Pararotalia nipponica*, '*P. taiwanica*' and '*P. ozawai*' all have a geological record extending back to the Miocene. They occur widely in the Indo-Pacific today.

Genus *PSEUDOROTALIA* Reiss & Merling, 1958

Type-species: *Rotalia schroeteriana* Parker & Jones *in* Carpenter, 1862.

Pseudorotalia schroeteriana (Parker & Jones)

Pl. 6, figs 1, 2; Pl. 10, figs 12, 13

1826 *Gyroidina conoides* d'Orbigny : 278, no. 9 (*nom. nud.*).
1853 *Faujasina* sp. Williamson : 87; pl. 10, figs 1–6.
1862 *Rotalia schroeteriana* Parker & Jones *in* Carpenter : 213; pl. 13, figs 7–9.
1884 *Rotalia schroeteriana* Parker & Jones; Brady : 707; pl. 115, figs 7a–c.
1893 *Rotalia schroeteriana* Parker & Jones; Egger : 422; pl. 19, figs 10–12.
1899 *Rotalia schroeteriana* Parker & Jones; Flint : 332; pl. 76, fig. 1.
1906 *Gyroidina conoides* d'Orbigny; Fornasini : 69; pl. 4, figs 8a, b (d'Orbigny's unpublished figures).
1927 *Rotalia schroeteriana* Parker & Jones; Hofker : 39; pl. 18, figs 1a–4; pl. 19, figs 1–12; pl. 21, figs 1, 2, 7, 11, 13.
1934 *Rotalia conoides* (d'Orbigny) Thalmann : 431; figs 2, 3a–c.
1936 *Rotalia schroeteriana* Parker & Jones; Keijzer : 132; pl. 4, figs 3–5, 7–10; text-fig. 26.
1937 *Rotalia conoides* (d'Orbigny); Yabe & Asano : 104; pl. 18, fig. 9.
1937 *Rotalia schroeteriana* Parker & Jones var. Yabe & Asano : 104; pl. 19, fig. 10.
1940 *Streblus schroeterianus* (Parker & Jones) Ishizaki : 59; pl. 3, figs 5a–6b, 9a–10b; pl. 4, figs 7, 8.
1956 *Rotalia conoidea* (d'Orbigny); Marks : 41; pl. 21, figs 43a–c.
1958 *Pseudorotalia schroeteriana* (Parker & Jones) Reiss & Merling : 13; pl. 1, figs 15–17; pl. 2, fig. 1; pl. 5, fig. 15.
1958 *Rotalia papillosa* Brady; Ganapati & Satyavati : 100 (list); pl. 5, figs 124, 125 (*non* Brady 1884).
1960 *Streblus schroeterianus* (Parker & Jones); Barker : 238; pl. 115, figs 7a–c (after Brady).
1962 *Rotalia conoides* (d'Orbigny); Visser & Hermes : 60, fig. 65a.
1964 *Pseudorotalia schroeteriana schroeteriana* (Parker & Jones); Huang : 60; pl. 1, fig. 12.
1968 *Pseudorotalia schroeteriana* (Parker & Jones); Hofker : 30; pl. 10, figs 4–18.
1968 *Pseudorotalia schroeteriana* (Parker & Jones); Bhalla : 384 : pl. 2, fig. 2.
1971 *Pseudorotalia schroeteriana* (Parker & Jones); Hofker : 31; pl. 73, figs 1–6; pl. 74, figs 1–11.

MATERIAL. 256 specimens. NB 9446, 9448, 9449, 9450, 9452, 9454, 9460.

VARIATION.	*Microspheric*	*Megalospheric*
Maximum diameter	0·90–1·14 mm	0·21–1·50 mm
Thickness	0·90–0·94 mm	0·20–1·20 mm
Number of chambers in first whorl	5	4–7
Number of chambers in second whorl	5–6	6–11
Number of chambers in last whorl	9–11	7–14

REMARKS. In the present material the microspheric form has a flat spiral and a high conical umbilical side with single or double rows of beading along the sutures. The umbilical plug is added to the apex of the newest chamber but because of the high conical test shape the plug development on earlier chambers remains prominent, simulating a lateral displacement, whereas it is in reality terminal in relation to each chamber. The majority of megalospheric specimens are similar to the microspheric (see Pl. 6, fig. 1; Pl. 10, fig. 12), but some show a tendency, previously noted by Keijzer (1936) and Hofker (1927, 1968 and 1971), to 'outgrow' this shape, and by adding additional whorls with convex peripheries a proportionately much lower test is produced with a truncate ventral apex (see Pl. 6, fig. 2; Pl. 10, fig. 13). The evidence of Keijzer and Hofker, together with our observations on material from the Malay Archipelago, leads us to conclude that the conical form (= '*Gyroidina conoides*' d'Orbigny) is typical of immature specimens and that adults tend to lose their conical shape. In addition to the variation described above, two large megalospheric forms in sample NB 9449 resemble *Asanoina globosa* (Yabe & Asano), but are less trochoid dorsally than the type figure.

The type-specimen of *Rotalia schroeteriana* could not be found despite an extensive search of the Parker & Jones and Carpenter Collections, whilst the only remaining specimen of Williamson's *Faujasina* sp. does not fit the ascribed figure (1853 : pl. 10, fig. 3) nor is a locality given. The single specimen recorded by Heron-Allen & Earland (1915) from Kerimba, Mozambique, has rather deeply incised sutures and is not considered conspecific wth those from the western Pacific. Belford's figured specimens from the Pliocene of Papua (1966 : pl. 70, figs 12–16), likewise, appear to belong to another species.

DISTRIBUTION. *Fossil*: Miocene (Yabe & Asano 1937), Pliocene (Thalmann 1934) and Pleistocene (Marks 1956) of Java; Pliocene of Papua (Hofker 1971) and Taiwan (Ishizaki 1940, Huang 1964); Plio-Pleistocene of western New Guinea (Irian) (Visser & Hermes 1962). *Recent*: Widespread in the tropical western Pacific from Taiwan to Australia and particularly common in the islands of the Malay Archipelago. Also reported from the Bay of Bengal.

Pseudorotalia catilliformis (Thalmann)

Pl. 6, figs 3–5; Pl. 10, figs 10, 11

1934 *Rotalia catilliformis* Thalmann : 437; pl. 11, figs 1–3d.
1937 *Rotalia catilliformis* Thalmann; Yabe & Asano : 104; pl. 19, fig. 10.
1937 *Rotalia tikutoensis* Nakamura : 141; pl. 12, figs 7a–c.
1940 *Streblus tikutoensis* (Nakamura) Ishizaki : 60; pl. 3, figs 14a, b; pl. 4, figs 12, 13 only.
1962 *Rotalia catilliformis* Thalmann; Visser & Hermes : 60, fig. 65c.
1964 *Pseudorotalia schroeteriana tikutoensis* (Nakamura) Huang : 61; pl. 2, figs 9a–c; pl. 3, figs 7, 8.
1966 *Pseudorotalia catilliformis* (Thalmann) Belford : 114; pl. 21, figs 4–10.
1968 *Pseudorotalia catalliformis* (Thalmann); Huang : 91; pl. 3, figs 15–17 (misspelling).
1975 *Pseudorotalia catilliformis* (Thalmann); Billman & Kartaadipura : 306; pl. 1, figs 4a–c.

MATERIAL. 398 specimens. NB ? 9449, 9450, 9452, 9453, 9454, 9455, 9456/7, 9460.

VARIATION.	*Microspheric*	*Megalospheric*
Maximum diameter	1·30–2·26 mm	1·22–1·60 mm
Thickness	0·50–0·74 mm	0·55–0·85 mm
Numbers of chambers in final whorl	16–27	13–23
Number of chambers in second whorl	6	10–17
Number of chambers in first whorl	5	5–10
Number of whorls not exceeding	4½	3½

REMARKS. The microspheric test of the Togopi specimens varies considerably in thickness. There are examples, in a large population in NB 9452, of the very thin specimens with slightly concave venters, as figured by Thalmann (1934), with gradation to the thicker form illustrated in Pl. 6, figs 4, 5, identical to *Rotalia tikutoensis* Nakamura. The plug is very large and highly perforate, usually opaque. The spire is generally low, the dorsal side being only slightly convex, some specimens in NB 9460, however, having a higher spire. The amount of beading on the sutures is variable.

The megalospheric test (Pl. 6, fig. 3) is much smaller, with an acute periphery, and is usually more trochoid. The ventral surface nevertheless is very flat.

Little comparative work has previously been undertaken on *R. catilliformis* and *R. tikutoensis*. The latter was first described from the Pliocene Byoritu beds of Taiwan and was separated from *R. catilliformis* by being less compressed, less concave ventrally and possessing fewer than 25 chambers in the final whorl. Huang (1964) was originally of the opinion that *R. tikutoensis* was a subspecies of *R. schroeteriana* Parker & Jones, but in 1968, having re-examined Nakamura's type, considered it to be synonymous with Thalmann's species, a conclusion with which we agree. We do not consider *Streblus tikutoensis* (Nakamura) of Chang (1960 : pl. 2, figs 13a–c), from the upper Miocene of Taiwan, to be conspecific with our material, but it may have affinities with *Rotalia indopacifica* Thalmann.

DISTRIBUTION. *Fossil*: Miocene of Java (Yabe & Asano 1937); Pliocene of Java (Thalmann 1934), Taiwan (Nakamura 1937, Huang 1964 and Ishizaki 1940) and Papua (Belford 1966); Plio-Pleistocene of western New Guinea (Irian) (Visser & Hermes 1962). Billman & Kartaadipura (1975) do not record *P. catilliformis* above the late Miocene in the Kutei Basin of east Borneo. Nevertheless, specimens of their *P. tikutoensis*, which they kindly sent to us from higher in Kerindingan Well no. 1, fall within the variation seen in our material, and thus extend the range of the species up into the Plio-Pleistocene of this area as well. *Recent*: *P. catilliformis* does not appear to be living in the Indo-Pacific today.

Pseudorotalia indopacifica (Thalmann)
Pl. 6, figs 6a–8b; Pl. 10, figs 7–9

1899 *Rotalia papillosa* Brady; Flint : 332; pl. 76, fig. 2 (*non* Brady 1884).
1921 *Rotalia schroeteriana* Parker & Jones; Cushman : 347; pl. 73, figs 1a–c (*non* Parker & Jones *in* Carpenter 1862).
1935 *Rotalia indopacifica* Thalmann : 605.
1940 *Streblus indopacificus* (Thalmann) Ishizaki : 54; pl. 3, figs 1a, b; pl. 4, figs 1–6.
1951*d* *Rotalia indopacifica* Thalmann; Asano : 13, text-figs 99, 100.
1957 *Rotalia indopacifica* Thalmann; Samaniego & Gonzales : 203; pl. 23, figs 10a–c.
1963 *Pseudorotalia indopacifica* (Thalmann) Huang : pl. 4, figs 23a, b.
1964 *Pseudorotalia indopacifica* (Thalmann); Huang : 60; pl. 1, figs 7a–c; pl. 3, fig. 4.
1970 *Pseudorotalia indopacifica* (Thalmann); Kim : 108 (table); pl. 2, figs 6a–c.

MATERIAL. 168 specimens. NB 9448, 9449, 9452, 9453, 9460.

VARIATION.	*Microspheric*	*Megalospheric*
Maximum diameter	0·96–2·10 mm	0·41–1·30 mm
Thickness	0·55–1·30 mm	0·28–0·80 mm
Number of chambers in final whorl	16–24	8–18 (usually 13–18)
Number of chambers in second whorl	6–8	7–14
Number of chambers in first whorl	4–6	5–7

REMARKS. Our material has been compared with specimens in the BM(NH) from Albatross Station D5313, China Sea (see Cushman's localities, 1921 : 347). In this sample the microspheric form attains 2·5 mm in diameter and appears to be identical with the type-figure. The megalospheric form is usually 1–2 mm in diameter and has 5–6, 10–11 and 14–16 chambers in the first, second and final whorls. It is either compressed, thus almost equally biconvex, or more highly trochoid dorsally. It has a small plug dissected into beadlets. In both generations the umbilical ends of the chambers have small hyaline flaps and the test is beaded along both spiral and cameral sutures. The canal system opens along the ventral sutures with a double row of pores, a feature characteristic of the genus. In sample NB 9460 some specimens ar ehighly trochoid dorsally, reminiscent of *Rotalia alveiformis* Thalmann (see Pl. 10, fig. 8), but the vast majority are closely similar to the topotypic specimens described above.

DISTRIBUTION. *Fossil*: Miocene of Taiwan (Huang 1963); Pliocene of Taiwan (Huang 1964), Japan (Asano 1951*d*) and the Philippines (Samaniego & Gonzales 1957). *Recent*: Philippines (Cushman 1921), Korean Yellow Sea (Kim 1970) and Taiwan (Ishizaki 1940); Flint's 'Albatross' locality is not recorded. Probably it is widespread in the Indo-Pacific at the present day, but has been confused with other species of *Pseudorotalia*.

Family **CALCARINIDAE** Schwager, 1876

Genus ***CALCARINA*** d'Orbigny, 1826

Type-species: *Nautilus spengleri* Gmelin, 1788.

Calcarina hispida Brady

Pl. 7, figs 1, 2; Pl. 10, fig. 14

1862 *Calcarina* sp. (hispid variety); Carpenter, Parker & Jones : 218; pl. 14, figs 6, 7.
1876 *Calcarina hispida* Brady : 589.
1884 *Calcarina hispida* Brady; Brady : 713; pl. 108, figs 8, 9.
1921 *Calcarina hispida* Brady; Cushman : 356; pl. 75, fig. 4.
1943 *Calcarina hispida* Brady; Gnanamuthu ; 18; pl. 4, figs 9a–c.
1954 *Calcarina hispida* Brady; Cushman, Todd & Post : 363; pl. 90, figs 9–12.
1959 *Calcarina hispida* Brady; Graham & Militante : 106; pl. 17, figs 5a–7b.
1959 *Calcarina spengleri* (Gmelin) Graham & Militante (*pars*) : 107; pl. 17, figs 8a, b, and 13a, b only.
1960 *Tinoporus hispidus* (Brady) Barker : 222; pl. 108, figs 8, 9.
1961 *Calcarina hispida* Brady; Huang : 88; pl. 5, figs 1–4, 20, 21.
1964 *Calcarina spengleri* (Gmelin); Le Roy : F40; pl. 5, fig. 3 (*non Nautilus spengleri* Gmelin 1788).
1965 *Calcarina hispida* Brady; Jell, Maxwell & McKellar : 277; pl. 44, figs 4a, b.
1968 *Calcarina hispida* Brady; Chiji & Lopez : 105; pl. 12, figs 8a, b.
1968 *Calcarina hispida* Brady; Antony : 100; pl. 7, fig. 8.
1970 *Calcarina hispida* Brady; Hofker : 63; pl. 43, figs 5–13; pl. 47, fig. 3.

MATERIAL. 118 specimens. NB 9449, 9450, 9460.

VARIATION. Greatest diameter up to 1·5 mm (excluding spines), thickness up to 0·7 mm. Number of whorls $1\frac{3}{4}$–$3\frac{1}{2}$, number of chambers in second whorl 9–14.

REMARKS. This highly variable suite of rather poorly preserved specimens closely resembles the *C. hispida/rustica* group. The chambers in the last whorl are prominent or obscure, while in cross section the test varies in its biconvexity, the chamber peripheries being either rounded or acute. The spines, never more than nine, arise at any angle along a suture and are always hispid, a character separating this species from *Calcarina spengleri* (Gmelin) and *C. quoyi* d'Orbigny. The strongly biconvex forms are usually heavily pustulate and very hispid, but flatter specimens with prominent chambers in the last whorl have reduced ornament, what pustules there are being confined to the umbilical region.

In comparison, *Calcarina mayori* Cushman has a less robust test with well-developed spines, while *C. rustica* Todd & Post has grooved spines. Nevertheless, it seems to us that much specific differentiation within this genus is more than usually arbitrary. Insufficient studies have yet been made on the internal structure and variation in external morphology of the test. In particular, we know little about how much spine development is affected by the environment.

DISTRIBUTION. *Fossil*: Pliocene of Okinawa (*C. spengleri* of Le Roy 1964). *Recent*: Widespread in the western Pacific from Japan to Queensland, Australia. Found also around India.

Family **ELPHIDIIDAE** Galloway, 1933

Subfamily **ELPHIDIINAE** Galloway, 1933

Genus ***ELPHIDIUM*** de Montfort, 1808

Type-species: *Nautilus macellus* Fichtel & Moll var. β Fichtel & Moll, 1798.

Elphidium cf. ***fax barbarense*** Nicol

Pl. 6, figs 14a, b

cf. 1944 *Elphidium fax barbarense* Nicol : 178; pl. 29, figs 10, 12.

MATERIAL. 11 specimens. NB 9449, 9452.

VARIATION. Maximum diameter 0·63–1·60 mm, thickness 0·33–0·38 mm. Plug diameter 0·18–0·35 mm. Number of chambers in last whorl 25–31.

REMARKS. Our specimens are characterized by a large number of retral bars per chamber and sutures which become strongly limbate towards the umbilicus; the plug usually has a central depression but is non-canaliculate. In apertural view the test is keeled with angular peripheries, while the aperture is a series of interiomarginal pores at the base of the face, with areal pores on older chamber faces.

The Togopi specimens seem closest to *Elphidium fax barbarense* of Nicol (1944), a subspecies first described from the Pleistocene of California, but differ in having a poreless plug and sutures which are limbate only at their umbilical ends. Furthermore, a number of different Indo-Pacific forms appear to have been included in Nicol's subspecies and there has been some confusion with *E. crispum* (Linné).

DISTRIBUTION. *E. fax barbarense* auctt. has been reported from Pliocene (Asano 1950) to Recent sediments in the Indo–west Pacific region.

Genus *CELLANTHUS* de Montfort, 1808

Type-species: *Nautilus craticulatus* Fichtel & Moll, 1798.

Cellanthus craticulatus (Fichtel & Moll)

Pl. 7, figs 1, 2a, b; Pl. 10, figs 15, 16

1798 *Nautilus craticulatus* Fichtel & Moll : 51; pl. 5, figs h, i, k.
1862 *Polystomella craticulata* (Fichtel & Moll) Carpenter : 279; pl. 16, figs 1–3, 7–9.
1884 *Polystomella craticulata* (Fichtel & Moll); Brady : 739; pl. 110, figs 16, 17a, b.
1893 *Polystomella craticulata* (Fichtel & Moll); Egger : 241; pl. 20, figs 24, 25.
1911 *Polystomella craticulata* (Fichtel & Moll); Schubert : 91, text-fig. 11.
1914 *Polystomella craticulata* (Fichtel & Moll); Cushman : 34; pl. 19, figs 4a, b.
1927 *Polystomella craticulata* (Fichtel & Moll); Hofker : 56; pl. 26, figs 10–15; pl. 27, figs 1–4; pl. 28, figs 4, 8, 10, 11.
1941*a* *Elphidium craticulatum* (Fichtel & Moll) Le Roy : 78; pl. 6, figs 34, 35.
1944 *Elphidium* aff. *craticulatum* (Fichtel & Moll); Le Roy : 24; pl. 8, figs 36, 37.
1950 *Elphidium craticulatum* (Fichtel & Moll); Asano : 7, text-figs 36, 37.
1954 *Elphidium craticulatum* (Fichtel & Moll); Kleinpell : 42; pl. 2, fig. 4.
1958 *Elphidium craticulatum* (Fichtel & Moll); Ganapati & Satyavati : 125 (list); pl. 3, figs 87, 88.
1959 *Elphidium craticulatum* (Fichtel & Moll); Graham & Militante : 74; pl. 11, figs 9–12b.
1960 *Elphidium craticulatum* (Fichtel & Moll); Barker : 228; pl. 110, figs 16, 17a, b (after Brady).
1961 *Elphidium craticulatum* (Fichtel & Moll); Braga : 127; pl. 13, figs 4, 5.
1963 *Elphidium craticulatum* (Fichtel & Moll); Huang : pl. 2, fig. 47.
1964 *Elphidium craticulatum* (Fichtel & Moll); Rocha & Ubaldo : 147; pl. 18, fig. 5.
1964*a* *Elphidium craticulatum* (Fichtel & Moll); Rocha & Ubaldo : 416; pl. 3, fig. 7.
1965 *Elphidium craticulatum* (Fichtel & Moll); Rocha : 420; pl. 5, fig. 3.
1965 *Elphidium craticulatum* (Fichtel & Moll); Jell, Maxwell & McKellar : 278; pl. 44, figs 7a, b.
1968 *Elphidium craticulatum* (Fichtel & Moll); Antony : 61; pl. 4, fig. 3.
1968 *Elphidium craticulatum* (Fichtel & Moll); Albani : 111; pl. 9, figs 19, 20.
1968 *Cellanthus craticulatus* (Fichtel & Moll) Chiji & Lopez : 105; pl. 13, fig. 9.
1971 *Cellanthus craticulatus* (Fichtel & Moll); Hofker : 171; pl. 101, figs 11–14; pl. 107, figs 1, 2, 7.

MATERIAL. 55 specimens. NB 9447, 9449, 9450, 9452, 9454, 9460.

VARIATION.	*Microspheric*	*Megalospheric*
Maximum diameter	1·15–4·50 mm	0·32–1·45 mm
Thickness	0·50–1·60 mm	0·32–0·85 mm
Plug diameter	0·50–3·20 mm	0·23–0·70 mm
Number of chambers in final whorl	31–60	25–28

REMARKS. A *Cellanthus* with large caniculate plug, spiral canal, double septa and diverging canals opening into a double row of pores along the sutures; see Hofker (1927, 1971) for internal morphological details.

Sexual dimorphism in the adult is pronounced, the large lenticular microspheric specimens, one of few fossil records of this dimorph, having a huge plug obscuring most of the test. In juvenile forms, however, sexual dimorphism can only be recognized in thin sections.

Elphidium javanum Yabe & Asano (1937 : 102; pl. 18, figs 10a, b), from the Miocene of western Java, and *E. taiwanum* Nakamura (1937 : 193; pl. 11, figs 9a, b), from the Neogene of Taiwan, may prove to be conspecific with *Cellanthus craticulatus* (Fichtel & Moll). Furthermore, *E. batavum* Hofker (1968 : 32; pl. 11, figs 8–19), from the Recent sediments of the Bay of Jakarta, Java, has doubtful validity. In 1968 Hofker stated that his new species was a true *Elphidium*, not a *Cellanthus*, forming a link between *E. crispum* and *C. craticulatus*, and cited Cushman's *E. craticulatum* from Tonga (1933: 48; pl. 11, fig. 5), as being conspecific. In 1971, however, he included this reference, without comment, in his synonymy of *C. craticulatus*.

DISTRIBUTION. *Fossil*: Miocene of the Bismarck Archipelago (Schubert 1911), western Java (Le Roy 1944) and Fiji (Kleinpell 1954); Late Tertiary (? Pliocene) of Siberoet Island, Indonesia (Le Roy 1941*a*); Pliocene of Japan (Asano 1950) and Taiwan (Huang 1963) and a sub-Recent raised beach in Timor (Rocha & Ubaldo 1964). *Recent*: A widely distributed shallow-water species in the western Pacific, from Japan to Australia, and Indian Oceans – the east coast of Africa, Arabian Gulf (type locality) and Indian coasts.

Cellanthus adelaidensis (Howchin & Parr)

Pl. 6, figs 13a, b; Pl. 10, figs 18, 19

1938 *Elphidium adelaidense* Howchin & Parr : 300; pl. 18, fig. 7; pl. 19, figs 5, 6.
1938 *Elphidium* sp. cf. *adelaidense* Howchin & Parr : 308; pl. 17, fig. 3.
1975 *Elphidium* sp. 14 Billman & Kartaadipura : 306; pl. 1, fig. 6.

MATERIAL. 41 specimens. NB 9449, 9450, 9452, 9460.

VARIATION.	*Microspheric* (1 specimen)	*Megalospheric*
Maximum diameter	2·55 mm	0·70–2·20 mm
Thickness	1·05 mm	0·18–0·90 mm
Number of whorls	$7\frac{3}{4}$	1–5
Number of chambers in first whorl	5	8–10
Number of chambers in second whorl	10	21–24
Number of chambers in third whorl	13	31–34
Number of chambers in final whorl	50	13–41
Proloculus internal diameter	?	0·15–0·32 mm

REMARKS. These specimens generally have only lightly developed bars covering the retral processes, and the very low chambers have their sutures so close together that double rows of pores of the sutural canal give the impression that the shell is highly perforate (see Pl. 6, fig. 13). There is no external difference between the two generations and only one microspheric form has been found. The septa in this species are double, their canal opening into the subsutural canal which branches near the surface to give biperforate sutural pores. The umbilical canals seldom anastomose and some appear to arise from a poorly-developed spiral canal. The plug is poorly developed for *E. adelaidense* but as other morphological details are very similar, we consider that the Togopi specimens are conspecific. *Elphidium rotatum* Howchin & Parr (1938 : 299; pl. 17, figs 1, 2, 4), a much compressed form, recorded from the Pliocene to Recent of Australia, appears to be the only other species in the Indo-Pacific similar in size and external morphology to our material.

DISTRIBUTION. *Cellanthus adelaidensis* does not appear to have been found later than the Pliocene. Howchin & Parr (1938) record it from the Miocene and Upper Pliocene of South Australia, while Billman & Kartaadipura (1975 : 306) state that in east Kalimantan, Borneo, their *Elphidium* sp. 14 'has it highest stratigraphical occurrence in the *Asanoina* Zone', which they interpret as Pliocene.

Cellanthus biperforatus sp. nov.

Fig. 61; Pl. 7, figs 3a, b; Pl. 10, fig. 21

DIAGNOSIS. A rotund *Cellanthus* with a large canaliculate plug. Sutures straight to gently curved, bearing on either side a row of sutural pits.

NAME. From the two rows of sutural pits, one on each side of the suture.

HOLOTYPE. BM(NH) reg. no. P50160, from NB 9452.

MATERIAL. 90 specimens. NB 9446, 9447, 9452, 9454, 9456/7, 9460.

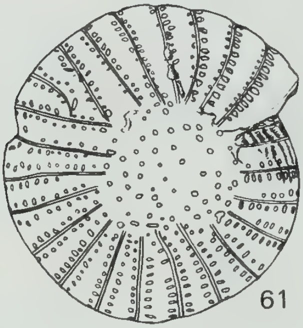


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Fig. 61 *Cellanthus biperforatus* sp. nov. P50160. Side view of **holotype** showing position of chamber sutures (see also Pl. 7, figs 3a, b). Sample NB 9452. ×40.

DESCRIPTION (Holotype). Test calcareous, perforate, biconvex and plugged. Plug raised, translucent, occupying a third of the test diameter and perforated by many canals. Periphery round in side view. Last whorl involute, made up of 24 non-lobate chambers with sutures which are radial to gently curved (slightly depressed in later chambers) and lined on each side by a row of pits containing the surface pores of the subsutural canal system. On the later-formed sutures the anterior pores are larger than the posterior row, but for the most part are of the same size. Test inflated in apertural view, peripheries subrounded. Apertural face low, aperture a row of 13 interiomarginal pores separated from each other by bars of secondary shell material which are developed on earlier whorls and extend in a subdued manner onto the first few chambers of the last whorl.

DIMENSIONS (Holotype). Maximum diameter 1·06 mm, thickness 0·65 mm, diameter of plug 0·45 mm.

VARIATION. Size range of paratypes: maximum diameter 0·32–1·40 mm, thickness 0·30–1·05 mm, plug diameter 0·40–1·15 mm.

Externally the two generations are not distinguishable. From sectioned megalospheric specimens the following chamber counts were made:

Chambers in first whorl	6–14
Chambers in second whorl	8–23
Chambers in third whorl	13–32
Chambers in last whorl	24–42

A maximum of six whorls has been counted in this species.

REMARKS. Our specimens superficially resemble the Neogene species *Elphidium taiwanum* Nakamura (1937 : 139; pl. 11, figs 9a, b) and *E. javanum* Yabe & Asano (1937 : 102; pl. 18, figs 10a, b), but differ in possessing on each side of the suture a row of sutural pits, each containing a pore which forms the surface extremity of the subsutural canal system. In the last two species, which are similar to *Cellanthus craticulatus* (Fichtel & Moll) except for their subdued retral ornament, the bifurcating subsutural canal reaches the surface of the test as pores in a single row of elongate sutural pits.

The very thin double septum, double sutural pores and large perforate plug are typical of *Cellanthus*.

Cellanthus hailei sp. nov.

Pl. 6, figs 9a, b; Pl. 10, fig. 22

DIAGNOSIS. An inflated *Cellanthus* with rounded peripheries, low apertural face and apparently poreless plug. Ornament of many retral bars per suture; those at the beginning of the final whorl anastomosing to give coarse striae.

NAME. In honour of Professor N. S. Haile, formerly of the Geological Survey of Malaysia, who collected the material described in this paper.

HOLOTYPE. BM(NH) reg. no. P50152, from NB 9452.

MATERIAL. 30 specimens. NB 9447, 9449, 9452, 9453, 9460.

DESCRIPTION (Holotype). Test round in outline, involute, margin entire; inflated and subovate in edge view, peripheries subrounded. There are 36 chambers in the final whorl with 10 retral bars per suture on each side on the first, and 21 on the last chamber of the whorl. The retral bars tend to branch and anastomose at the beginning of the final whorl to give crude striae, but are distinctly separate from the next row of bars after about 10 chambers. Sutures gently curved and slightly limbate later. Umbilical plug distinct and raised but feebly dissected; one or two pits are present but there seem to be no true pores. Apertural face low, aperture indistinct, probably a series of interiomarginal pores.

DIMENSIONS (Holotype). Maximum diameter 1·40 mm, thickness 0·84 mm. Height of apertural face 0·09 mm. Diameter of plug 0·40 mm.

VARIATION. Size range of paratypes: diameter 0·40–1·50 mm, thickness 0·70–1·05 mm. Diameter of plug 0·18–0·45 mm. The number of retral bars per suture on each side of the test varies from 6 to 20, the number of whorls from 3 to 6 and the number of chambers per whorl as seen in section is as follows:

	Microspheric	*Megalospheric*
First whorl	7	10–14
Second whorl	10–11	23–27
Last whorl	28–34	25–40

The internal proloculus diameter is 0·01 mm in the microspheric form and between 0·13 and 0·22 mm in the megalospheric.

REMARKS. In both generations, determinable only in thin section, the coiling is tight with little increase in the chamber width throughout. The septa are double and carry a broad canal which opens as a rectangular single pore at the surface. This canal system does not penetrate the wedge-shaped plug, which is composed of numerous laminated layers and causes offlap of the newly formed chambers (see Pl. 10, fig. 22). The presence of a double septum places our new species in *Cellanthus*, but the apparent absence of umbilical canals and double sutural pores is inconsistent with the classification (Loeblich & Tappan 1964) used here. The aperture, often seen best in vertical thin sections, is a single row of large interiomarginal pores.

Cellanthus hailei sp. nov. has the striate ornamentation of the early chambers of the final whorl so characteristic of the *Elphidium indicum/hispidulum* group, together with the general test morphology of *Cellanthus craticulatus* to which it is most closely related. It differs from *C. craticulatus* (and *E. batavum* Hofker), however, in possessing a non-perforate plug and a partially striate test; furthermore, it does not have a keel.

Genus ***CRIBROELPHIDIUM*** Cushman & Brönnimann, 1948

Type-species: *Cribroelphidium vadescens* Cushman & Brönnimann, 1948.

Cribroelphidium dentense sp. nov.

Pl. 7, figs 4a, b

DIAGNOSIS. A robust *Cribroelphidium* with inflated later chambers and keeled only in the earlier part of the last whorl. Pustulose septal pits strongly developed and elongate in later part of test; up to 14 septal bars per suture on each side. Apertural face very broad.

NAME. Described from the Dent Peninsula, Sabah.

HOLOTYPE. BM(NH) reg. no. P50161, from NB 9452.

MATERIAL. 64 specimens. NB 9452.

DESCRIPTION (Holotype). Test involute, perforate, periphery in side view smoothly curved in early part of final whorl, becoming slightly lobate later. Chambers, 11 in number, only gradually increasing in size; early chambers keeled, later ones unkeeled and moderately inflated. Sutures curved, depressed and crossed by strong bars of shell material which in the later chambers do not completely bridge the sutures; between the bars are septal pits (fossettes), the floors of which are finely pustulate. Umbilical region slightly depressed with a faintly rugose plug associated in the earlier portion of the final whorl with the thickened umbilical ends of the chambers. In apertural view the test is moderately compressed, the periphery of the earlier part of the final whorl being subrounded, that of the apertural face broadly rounded. Apertural face convex, almost as high as wide, with distinct basal interiomarginal pores separated by bars; small areal pores surrounded by pustules are also present.

DIMENSIONS (Holotype). Maximum diameter 0·50 mm, thickness at centre 0·21 mm. Height of apertural face 0·21 mm, width 0·28 mm.

VARIATION. Size range of paratypes: maximum diameter 0·33–0·70 mm, thickness across last chamber 0·33–0·70 mm, thickness across umbilicus 0·15–0·35 mm. The number of chambers in the first whorl varies between 6 and 9, those in the last whorl between 10 and 11. Since the initial part of the coil is tight there is no way of distinguishing the two generations externally.

REMARKS. Closely related to the *Elphidium articulatum/excavatum* group, but differs in its less lobate periphery, partial development of a keel, more numerous fossettes, more inflated test and much wider apertural face. The new species also resembles in side view *Elphidium kusiroense* Asano from the Pleistocene of Japan (Asano 1938 : 590; pl. 14, fig. 2), but in apertural view is markedly different – the latter is very compressed and does not have a keel on the early part of the final whorl.

Because of the absence of a well-defined canal system, presence of sutural bars, single septa and both interiomarginal and areal pores on the apertural face, the species is placed in *Cribroelphidium.*

Genus *CRIBRONONION* Thalmann, 1947

Type-species: *Nonionina heteropora* Egger, 1857.

Cribrononion reticulosus (Cushman)
Pl. 6, fig. 12

1933 *Elphidium reticulosum* Cushman : 51; pl. 12, figs 5a, b.
1939 *Elphidium reticulosum* Cushman; Cushman : 59; pl. 16, figs 24a, b.
? 1957 *Elphidium hyalocostatum* Todd : 300; pl. 88, figs 19a, b.
1969 *Elphidium* sp. A cf. *E. milletti* (Heron-Allen & Earland); Betjeman : 130; pl. 18, figs 8, 9.
1970 *Elphidium reticulosum* Cushman; Matoba : 52; pl. 6, figs 12a, b.
? 1970 *Elphidium* cf. *reticulosum* Cushman; Matoba : 52; pl. 6, figs 13a, b.

MATERIAL. 70 specimens. NB 9447, 9449, 9450, 9452, 9454.

VARIATION. Maximum diameter 0·30–0·58 mm, maximum thickness 0·15–0·23 mm. Number of chambers in first whorl 7–9, in second 8–13 and in final whorl 9–12.

REMARKS. A tightly coiled, somewhat compressed species with retral bars strongly developed on the earlier chambers, the final chambers being covered with 'a fine network of irregular pattern' as described by Cushman (1933: 51). The plug area consists of plates (or layers) of crystalline material; no canals are visible. The later chambers of a number of specimens in the Togopi samples have a tendency to become strongly inflated as in the type-figure, but our illustrated specimen (Pl. 6, fig. 12) is more usual. Internally there are no diverging canals emanating from the intraseptal subsutural canal system. The aperture on the final chamber is a series of pores at the base of the apertural face; on earlier chambers it appears as an interiomarginal slit. These characters signify *Cribrononion*.

Forms very close to *Elphidium hyalocostatum* Todd occur in our samples and these would seem to be no more than a variety of *E. reticulosum* with stronger and more aligned ornamentation on the final chambers. We have examined the types of *E. milletti* (Heron-Allen & Earland) and note that they include specimens distinct from Cushman's species. The characteristic chevron ornament is particularly well developed on later chambers, and the periphery is strongly lobate when seen in side view (see Heron-Allen & Earland 1915: 735; pl. 53, figs 38–42). Murray's *E. reticulosum* from the Persian Gulf (1970: fig. 9C) would appear to belong to *E. milletti*.

DISTRIBUTION. Previously found only in the Recent of Japan (Matoba 1970), Saipan (Todd 1957), Tonga (Cushman 1933, 1939) and Western Australia (Betjeman 1969).

Cribrononion tikutoensis (Nakamura)
Pl. 6, figs 10a, b

1937 *Elphidium tikutoensis* Nakamura: 139; pl. 11, figs 10a, b.
1962 *Elphidium tikutoensis* Nakamura; Huang: 194; pl. 1, figs 1, 4b.
? 1967 *Cellanthus tungliangensis* Huang: 137; pl. 1, figs 1a, b; pl. 2, figs 2a, b.
1968 *Cellanthus tikutoensis* (Nakamura) Huang: 88; pl. 4, fig. 1.

MATERIAL. 54 specimens. NB 9450, 9452, 9454, 9460.

VARIATION. Maximum diameter 0·32–0·62 mm, thickness 0·18–0·25 mm. Number of chambers in first, second and final whorls 6–8, 9–12 and 11–15, respectively. Internal proloculus diameter 0·03–0·04 mm.

REMARKS. The umbilical region of our specimens is usually surrounded by enlarged sutural pores and the plug is variously developed, sometimes covered by secondary granulate shell material and often so reduced that the test appears evolute. The presence of interiomarginal pores and the simple canal system place it in *Cribrononion*. Nakamura's type-figure shows, however, a narrow interiomarginal slit-like aperture, a feature which is not commented on in either of Huang's redescriptions of the types (1962, 1967). *Cellanthus tungliangensis* Huang, from the Plio-Pleistocene of Penghu Island, off Taiwan, seems to differ very little from *E. tikutoensis* Nakamura; it certainly has small pores at the base of the apertural face and could well be conspecific.

DISTRIBUTION. Previously known only from the Neogene of Taiwan.

Genus *ELPHIDIELLA* Cushman, 1936

Type-species: *Polystomella arctica* Parker & Jones *in* Brady, 1864.

Elphidiella indopacifica Germeraad
Pl. 7, figs 5–7; Pl. 10, fig. 20

1946 *Elphidiella indopacifica* Germeraad: 67; pl. 3, figs 3, 4.

MATERIAL. 205 specimens. NB 9446, 9447, 9450, 9452, 9454, 9460.

VARIATION. Maximum diameter 0·41–1·45 mm, thickness 0·20–0·80 mm. Number of chambers in first whorl 7–9, in second 9–12 and in last whorl 9–26.

REMARKS. 'Differs from all known Elphidiellas by the large number of chambers' writes Germeraad (1946) in his description of this distinctive species, which surprisingly does not appear to have been recorded since. Our larger specimens, few in number and microspheric (Pl. 7, fig. 5), agree closely with his figures both in side and apertural view.

Most of our specimens, however, are much smaller (diameter less than 0·85 mm) and those sectioned proved to be megalospheric. These tests (Pl. 7, figs 6, 7) are robust and stout, but their peripheries are more acute and the number of chambers in the final whorl never exceeds thirteen. They nevertheless show the characteristic double row of alternating pits at each suture (the anterior set is the longest) and are thus conspecific. Germeraad had only two specimens and described only the microspheric form.

Because of the double row of sutural pores, interioareal multiple apertures and lack of retral processes the species is retained in *Elphidiella* despite the absence of a well-developed canal system.

DISTRIBUTION. Germeraad (1946) recorded *E. indopacifica* from the Recent of the Island of Ceram, Indonesia.

Subfamily **FAUJASININAE** Bermúdez, 1953

Genus ***PARRELLINA*** Thalmann, 1951

Type-species: *Polystomella imperatrix* Brady, 1881.

Parrellina hispidula (Cushman)

Pl. 6, fig. 11

1936 *Elphidium hispidulum* Cushman: 83; pl. 14, figs 13a, b.
1968 *Elphidium hispidulum* Cushman; Chiji & Lopez: 106; pl. 13, fig. 3.
1968 *Elphidium hispidulum* Cushman; Chiji: 62; pl. 3, fig. 12.
1968 *Parrellina hispidula* (Cushman) Hofker: 31; pl. 11, figs 1–7.

MATERIAL. 30 specimens. NB 9446, 9447, 9450.

VARIATION. Maximum diameter 0·30–0·65 mm, thickness 0·17–0·33 mm. Number of chambers in first, second and final whorl, 6–7, 10–12 and 9–15 respectively.

REMARKS. These specimens fall within the *E. hispidulum/indicum* group and differ from *E. reticulosum* Cushman in being inflated, plugged, hispid and non-reticulate. *Elphidium hokkaidoense* Asano (1950: 8, text-figs 44, 45) from the Pliocene of Japan is probably synonymous as it is said to differ from *E. indicum* Cushman in 'having weak costae nearly parallel to the periphery of earlier chambers', a feature also common to *E. hispidulum. E. indicum* has a large raised plug while *E. hispidulum* and *E. hokkaidoense* do not.

There are no true retral processes present in our specimens and in thin section the septal canal can be seen to branch within the spiral septa forming connections with more than one of the large pores traversing the wall. This type of canal system is typical of *Parrellina* (see Hofker 1968: 31).

DISTRIBUTION. *Fossil*: Pleistocene of Japan (Chiji 1968). This range would possibly be extended back into the Pliocene if *E. hokkaidoense* Asano proved to be conspecific. *Recent*: Australia (Cushman 1936), Java (Hofker 1968) and Japan (Chiji & Lopez 1968).

Family **NUMMULITIDAE** de Blainville, 1825

Subfamily **NUMMULITINAE** de Blainville, 1825

Genus ***NUMMULITES*** Lamarck, 1801

Type-species: *Camerina laevigata* Bruguière, 1792.

Barnett (1974), after studying 58 species of the Nummulitidae including *Nummulites willcoxi* Heilprin, the type-species of *Operculinoides* Hanzawa, concluded that *Operculinoides* is a superfluous generic name and that *Assilina, Operculina* and *Operculinella* are distinct from *Nummulites.*

Nummulites cf. ***amplicuneatus*** (Cole)

Pl. 9, figs 6–9; Pl. 10, fig. 26

cf. 1954 *Operculinoides amplicuneata* Cole: 573; pl. 204, figs 7, 9, 17, 18.

MATERIAL. Over 270 specimens. NB 9452.

VARIATION. Maximum diameter 1·9–3·7 mm, thickness 0·9–1·6 mm. Internal proloculus diameter 0·10–0·20 mm. Number of whorls 3–4¾. Number of chambers in first, second and third whorls 6–7, 11–15 and 18–21 respectively.

REMARKS. Only the involute and tightly coiled megalospheric generation is present. It has an acute edge, strong marginal cord and radiate or sinuous, flush sutures. Pustules are rarely present between sutures.

Although our specimens closely resemble *Nummulites amplicuneatus* (Cole), other externally similar species are *N. bikiniensis* (Cole) and *N. rectilatus* (Cole), from the Upper Miocene and Plio-Pleistocene respectively of Bikini Atoll, though neither of these has an acute peripheral margin.

DISTRIBUTION. *N. amplicuneatus* was recorded by Cole (1954) from the uppermost Miocene of Bikini Atoll, west Pacific.

Nummulites tamanensis (Vaughan & Cole)
Pl. 9, figs 13–16; Pl. 10, fig. 25

1941 *Operculinoides tamanensis* Vaughan & Cole: 43; pl. 10, figs 9, 10; pl. 11, figs 8–10; pl. 12, figs 1–3.

MATERIAL. 128 specimens. NB 9452.

VARIATION. Diameter 2–9 mm (megalospheric form 2–5·5 mm). Thickness not exceeding 1 mm. Internal proloculus diameter: microspheric form 0·03–0·15 mm, megalospheric 0·12–0·22 mm. Number of chambers in the first whorl: 7–8 (microspheric), 5–6 (megalospheric); second whorl: 10–12 (microspheric), 10–15 (megalospheric).

REMARKS. The present specimens are complanate to lenticular in shape, the umbo usually being more prominent on one surface than the other; the slowly unwinding coil has not been observed to flare in the microspheric form. Thin sections demonstrate the presence of trabeculae-like structures, which externally can be seen only faintly in the chamber walls of complete specimens but which have been shown by scanning electron microscopy of fractured specimens to be solid and to occupy the whole thickness of the wall. These 'trabeculae', which run anteriorly, normal to the septum, and have been observed to branch and even become arborescent (Pl. 10, fig. 25), are certainly present from the third chamber onwards and may occur back to the proloculus.

Our material has been compared directly with the types of *Operculinoides tamanensis* Vaughan & Cole (USNM nos 545879, 546154–7), the only observable difference being that the proloculus in the American specimens is smaller, having an internal diameter of 0·08–0·09 mm. We know of no other post-Oligocene species of *Nummulites* from the Indo–west Pacific region which shows these characteristic 'trabeculae', the function of which is unknown.

DISTRIBUTION. Originally described from the Lower Miocene of Trinidad; it does not appear to have been recorded subsequently.

Genus ***OPERCULINA***[3] d'Orbigny, 1826

Type-species: *Lenticulites complanatus* Defrance, 1822.

Van der Vlerk & Bannink (1969) suggested that the relative ages of deposits containing *Operculina* could be determined by calculating the value of 'factor E', this being a measure of the extent to which the second chamber is enclosed by the third

$$\left(\frac{\text{angle e}^1}{\text{angle e}^2} \times 100\right).$$

---

[3] See comments on *Nummulites*, p. 88.

They observed a significant decrease in the grade of enclosure in specimens from rocks of Eocene age through to those living today and plotted the rate of change of 'factor E' on a graph (see van der Vlerk & Bannink 1969 : fig. 3).

Operculina ammonoides (Schröter) and *O. bartschi* Cushman from the Togopi Formation have been used to test this hypothesis. Our two nummulitids, *Nummulites* cf. *amplicuneatus* (Cole) and *N. tamanensis* (Vaughan & Cole), were also measured although we are aware that 'factor E' might not be applicable to them since van der Vlerk & Bannink studied only *Operculina*. Twenty good thin sections of each species, all from sample NB 9452, were measured using the prescribed method, the angles e^1 and e^2 being measured separately by both of us and the arithmetic mean calculated. Fig. 62 shows the percentage distribution of 'factor E' expressed in histograms (compare with van der Vlerk & Bannink 1969 : fig. 2) and the calculated mean values for the four species. It can be seen that *O. bartschi* and *N. tamanensis* give very different and much lower results than *O. ammonoides* and *N.* cf. *amplicuneatus*, which although producing almost identical means, have contrasting histogram patterns.

Measurements were also made of three other species of known age and plotted (Fig. 63) together with the four Togopi species. *Operculina heberti* Munier-Chalmas (12 specimens) from

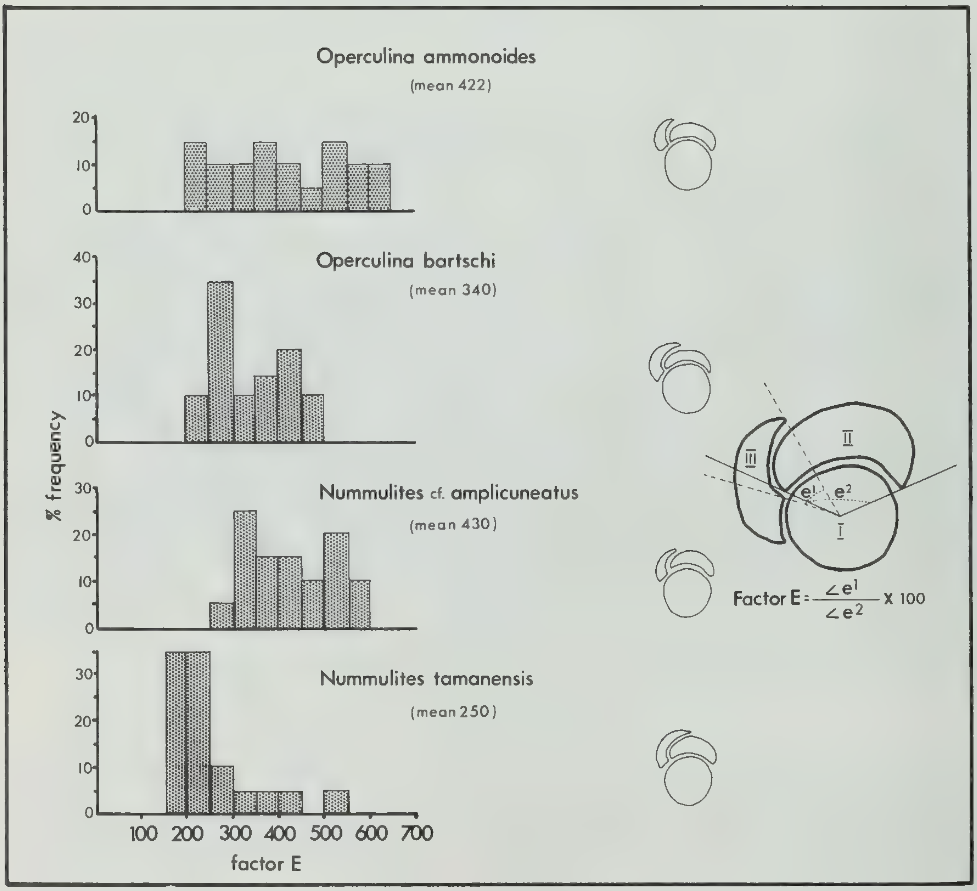


Fig. 62 Left: Percentage distribution of factor E in four species of *Operculina* and *Nummulites*, sample NB 9452, Togopi Formation. Twenty thin sections were measured in each case. Right: Method of measuring factor E from thin sections of megalospheric forms (after van der Vlerk & Bannink 1969). The degree of enclosure of chamber II by chamber III is shown for a typical member of each species to the left of this.

the Palaeocene of France gave an 'Oligocene' date, an *Operculinella* (10 specimens) from the Middle Miocene part of the Sebahat Formation (see p. 5) gave a fairly accurate result, while 11 Recent specimens of *Operculina ammonoides* (Schröter) in the Heron-Allen & Earland Collection, from Singapore Roads, produced a result slightly higher than that of van der Vlerk & Bannink's Recent species (Fig. 63). The Togopi specimens of *O. ammonoides* and *N.* cf. *amplicuneatus* both indicated an Upper Pliocene age; unfortunately *O. bartschi* gave an early Miocene date while *N. tamanensis* suggested a late Eocene age. This exercise did not, therefore, confirm the stratigraphical value of 'factor E' and further work is obviously necessary. It may be that the rate of evolution varies from one lineage to another, and in this connection it is noteworthy that the two tightly coiled Togopi nummulitids, although belonging to different genera, apparently produced a reliable date while the species with flaring coils did not. Unfortunately van der Vlerk & Bannink did not identify the species in their study.

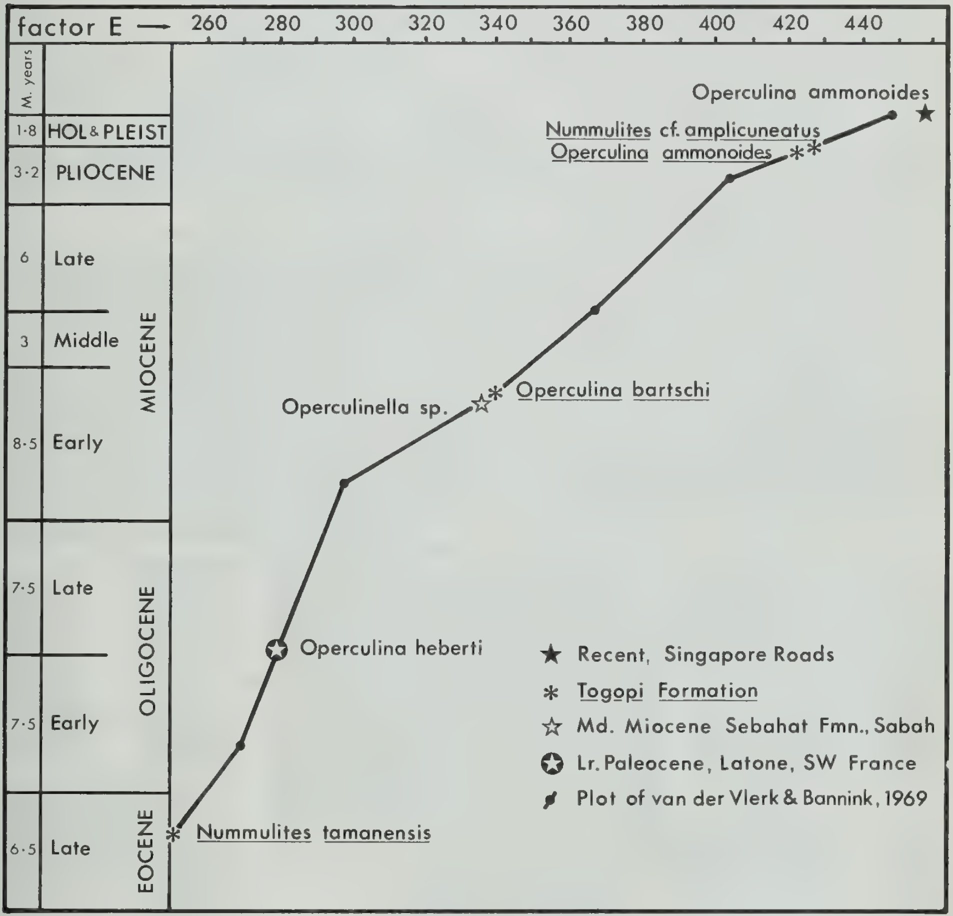


Fig. 63 The mean values of factor E for the four species of *Operculina* and *Nummulites*, together with those of three comparative species of known age, plotted on van der Vlerk & Bannink's (1969) graph of the rate of evolution of factor E but with time scale modified after Eysinga (1975). (Compare with fig. 3 of van der Vlerk & Bannink 1969.)

Operculina ammonoides (Schröter)
Pl. 9, figs 1–5; Pl. 10, figs 23, 27

1781 *Nautilus ammonoides* Gronovius : 282; pl. 19, figs 5, 6.
1783 *Nautilus ammonoides* Schröter : 21.
1860 *Operculina* sp. Carpenter : 12; pl. 3, figs 1, 2.
1893 *Operculina ammonoides* (Gronovius) Egger : 242; pl. 20, figs 38, 39.
1921 *Operculina discoidalis* (d'Orbigny); Cushman : 379 (see Cole 1961 : pl. 14, fig. 1).
1921 *Operculina granulosa* Leymerie; Cushman : 381 (see Cole 1961 : pl. 14, fig. 23).
1924 *Operculina gaimardi* d'Orbigny; Cushman : 50; pl. 17, fig. 4.
1925 *Operculina* (*Operculinella*) *venosa* (Fichtel & Moll); Yabe & Hanzawa : 49; pl. 5, figs 5–9, 19–27 only.
1933 *Operculina granulosa* Leymerie (?); Cushman : 56; pl. 14, figs 1–7b; pl. 15, figs 3–6 only; pl. 16, figs 1–3.
1935 *Operculinella venosa* (Fichtel & Moll); Hanzawa : 23; pl. 1, figs 31, 32, 34 only.
1938 *Operculina ammonoides* (Gronovius); Chapman & Parr : 290; pl. 17, figs 12–16; text-fig. 1, no. 5.
1939 *Operculina ammonoides* (Gronovius); Hanzawa : 229; pl. 15, figs 1a–2b only.
1946 *Operculinella venosa* (Fichtel & Moll); Abrard : 12; pl. 1, figs 5–6.
1948 *Operculina ammonoides* (Gronovius); Bannink : 81; pl. 5, figs 30, 31, 34–37; pl. 7, figs 46–48, 52, 53; pl. 8, figs 55, 56; pl. 11, figs 96–98; pl. 12, figs 99–101; pl. 13, figs 115–120; pl. 15, figs 133–142; pl. 17, figs 155–157, 164, 165; pl. 18, figs 168–170; pl. 19, figs 177–183.
1949 *Operculina gaimardi* d'Orbigny; Said : 14; pl. 2, fig. 37.
1954 *Operculina ammonoides* (Gronovius); Cushman, Todd & Post : 346; pl. 87, fig. 1.
1959 *Operculina ammonoides* (Gronovius); Cole : 356; pl. 28, figs 4–10; pl. 29, figs 3–15; pl. 30, figs 2–6, 8 only; pl. 31, figs 5–7.
1959 *Operculina ammonoides* (Gronovius); Graham & Militante : 76; pl. 12, figs 1, 2.
1960 *Operculina ammonoides* (Gronovius); Smout & Eames : 110 (see Cole 1959 : pl. 29, figs 3, 7, 12; pl. 31, figs 5–7).
1960 *Operculina hanzawai* Smout & Eames : 110 (see Cole 1959 : pl. 29, fig. 9).
1960 *Operculinella venosa* (Fichtel & Moll); Smout & Eames : 111 (see Cole 1959 : pl. 28, figs 8, 9; pl. 29, figs 6, 8, 10; pl. 30, figs 2, 6, 8).
1961 *Camerina ammonoides* (Gronovius) Cole : 118; pl. 14, figs 1–17, 20, 22–24 only; pl. 15, figs 2–6, 11 only.
1961 *Operculina ammonoides* (Gronovius); Huang : 86; pl. 3, figs 22, 23.
1964 *Operculina ammonoides* (Gronovius); Rocha & Ubaldo : 156; pl. 19, fig. 13.

MATERIAL. Over 220 specimens. NB 9447, 9449, 9450, 9452, 9453, 9454, 9460.

VARIATION.	*Microspheric forms*	*Megalospheric forms*
Maximum diameter	3–5 mm	0·6–3 mm
Thickness	up to 0·72 mm	0·25–0·65 mm
Internal proloculus diameter	0·02–0·03 mm	0·05–0·11 mm
Number of chambers in first whorl	5–7	6–8
Number of chambers in second whorl	10–12	9–13

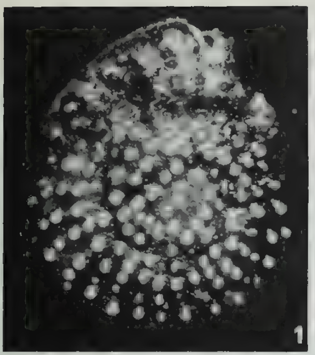
Plate 9 Light microscopy, magnifications approximate

Figs 1–5 *Operculina ammonoides* (Schröter). Figs 1, 5, P50194, P50198. Megalospheric forms, external views. Fig. 4, P50197. Megalospheric form, horizontally split specimen. Fig. 2, P50195. Microspheric form, horizontally split specimen. Fig. 3, P50196. Microspheric form, external view. All from sample NB 9452. ×15.

Figs 6–9 *Nummulites* cf. *amplicuneatus* (Cole). Megalospheric forms. Figs 6, 7. P50199, P50200. Horizontally split specimen and external view of test. Figs 8, 9. P50201, P50202. Block half-sections (vertical). All from sample NB 9452. ×10.

Figs 10–12 *Operculina bartschi* Cushman. External views. Fig. 10, P50203. Microspheric form. Figs 11, 12, P50204, P50205. ? Megalospheric forms. All from sample NB 9452. ×6.

Figs 13–16 *Nummulites tamanensis* (Vaughan & Cole). Figs 13, 14, P50206, P50207. Megalospheric forms; external view of test and horizontally split specimen. In Fig. 13 the 'trabeculae' characteristic of this species can just be seen externally, running normal to the later-formed sutures. Figs 15, 16, P50208. Microspheric form; external view of one half of test and internal view of other half, horizontally split. All from sample NB 9452. ×6.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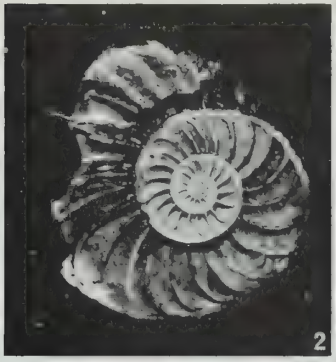
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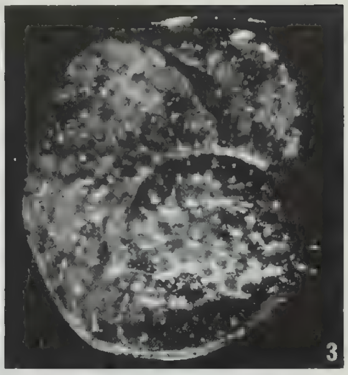
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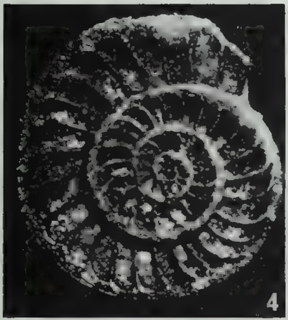
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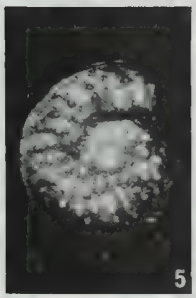
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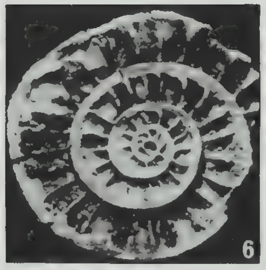
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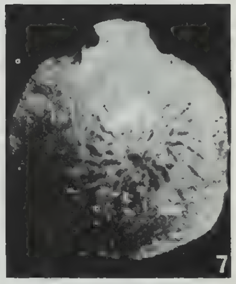
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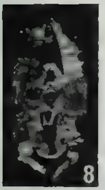
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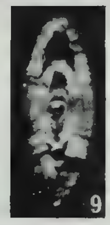
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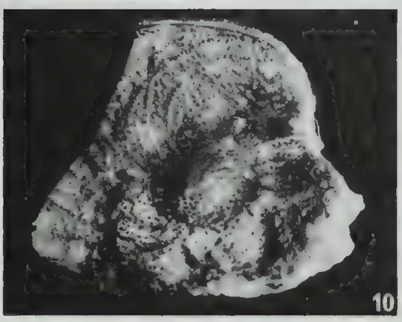
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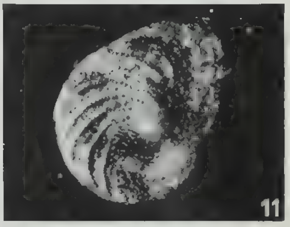
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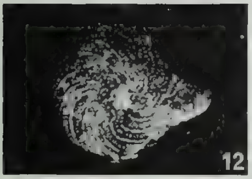
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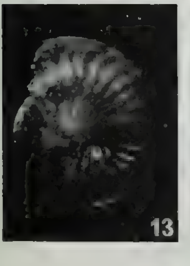
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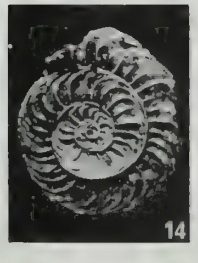
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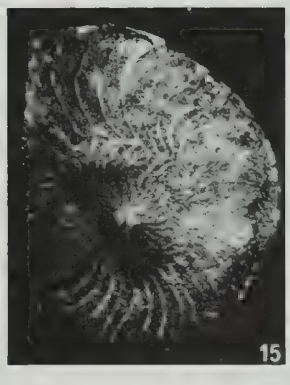
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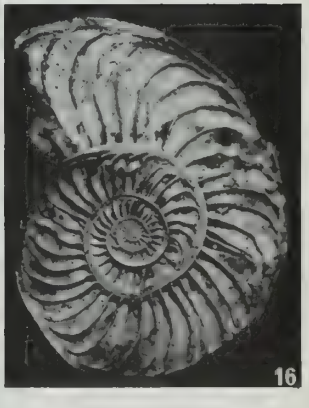
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REMARKS. This species was first described and figured by Gronovius (1781), but following Hemming (1954 : 283) the diagnosis of *Nautilus ammonoides* given by Schröter in 1783 is now taken as the first valid description, Gronovius' rather poorly illustrated specimens being the types. The inadequate description and illustrations have caused much confusion, and for many years *Hyalinea balthica* (Schröter) was regarded as *O. ammonoides*. Chapman & Parr (1938), Carter (1953), Smout & Eames (1960) and Cole (1959, 1961) all redefined the species, but there still remains great difficulty in setting a limit on intraspecific variation, which is doubtless governed by ecological factors. Cole and Smout & Eames disagree on whether there is a continuous variation between evolute and involute tests and on what constitutes *Operculinella venosa* (Fichtel & Moll). However, as these protagonists agree with Chapman & Parr's (1938) redefinition, we base our identification of *Operculina ammonoides* primarily on the latter's diagnosis.

The numerous specimens in Togopi sample NB 9452 show gradation from thin, almost evolute tests (supposedly mature) with a strong marginal cord, to thick, nearly involute immature tests, but never to completely involute '*Operculinella venosa*'-like forms. The megalospheric generation remains close-coiled but the microspheric has a flared last whorl (see Pl. 9). Both generations have a coarsely pustulate umbilical area with a large central umbonal pustule. In the final whorl, coarse beading commonly occurs on chambers or sutures, or both, being occasionally restricted to the chambers only, or to the early sutures.

The morphotypes represented by the following have not been seen in our material and are not, therefore, included in our synonymy, although regarded by some authors as synonymous with *O. ammonoides*.

Operculinella venosa (Fichtel & Moll); Cushman 1924.
? *Operculina ammonoides* (Gronovius); Carter 1953 : pl. 34, figs 4–6.
Operculina elegans Cushman 1921 : pl. 97, fig. 3.
Operculina discoidalis (d'Orbigny) var. *involuta* Cushman, 1921.
Nummulina discoidalis d'Orbigny, 1826.
Assilina nitida d'Orbigny, 1826.
Operculina gaymardi d'Orbigny, 1826.
Operculina gaimardi d'Orbigny; Cushman 1933 : pl. 13, figs 1–5.
Operculina philippinensis Cushman; Yabe & Hanzawa 1930 : pl. 12, fig. 9.
Operculina ammonoides (Gronovius); Chiji & Lopez 1968 : pl. 13, fig. 10.
Operculina sp. Puri 1957 : pl. 13, figs 1–14.
Operculinoides sp. Puri 1957 : pl. 13, figs 5–8.
Those specimens renamed by Barker (1960 : pl. 112) as *Operculina ammonoides* from Brady (1884).

DISTRIBUTION. *Fossil*: Miocene (Tf) of Borneo (Cole 1959); Neogene of Okinawa and Taiwan (Hanzawa 1935); post-Pliocene of Okinawa (Yabe & Hanzawa 1925, Cole 1959); ? Pleistocene of the Ryukyus (Cole 1959); Quaternary of the New Hebrides (Abrard 1946) and Timor (Rocha & Ubaldo 1964). Bannink (1948) records this species from numerous borings in Indonesia of Miocene age and younger. *Recent*: Widespread in the Indian and Pacific Oceans, the Red Sea and the Persian Gulf.

Operculina bartschi Cushman
Pl. 9, figs 10–12; Pl. 10, fig. 24

1860 *Operculina* sp. Carpenter : 12; pl. 3, figs 6, 11, 12 only; pl. 4, figs 1–4, 6, 10, 11.
1901 *Operculina* sp. Yoshiwara : pl. 1, figs 1, 2.
1921 *Operculina bartschi* Cushman : 376, text-fig. 13.
1925 *Operculina bartschi* Cushman var. *punctata* Yabe & Hanzawa : 52; pl. 6, figs 13–15; pl. 7, figs 13–18.
1925 *Operculina bartschi* Cushman; Yabe & Hanzawa : 52; pl. 6, figs 6–12; pl. 7, figs 11, 12.
1935 *Operculina bartschi* Cushman; Hanzawa : 22; pl. 2, figs 1–12.
1938 *Operculina bartschi* Cushman; Chapman & Parr : 292; pl. 17, figs 17, 18 only; text-fig. 6.
1946 *Operculina bartschi* Cushman; Abrard : 99; pl. 1, figs 3, 4.
1959 *Operculina bartschi* Cushman; Cole : 360; pl. 28, fig. 16.

MATERIAL. Over 260 specimens. NB 9450, 9452.

VARIATION.	*Microspheric forms*	*Megalospheric forms*
Maximum diameter	3–9 mm	3–6 mm
Thickness	up to 1 mm	up to 1 mm
Proloculus (internal) diameter	0·02 mm	0·11–0·25 mm
Number of chambers in first whorl	6–7	4–7
Number of chambers in second whorl	9–11	10–13
Number of chambers in third whorl	23–37	14–25

REMARKS. The chambers are high and narrow (sometimes malformed), arcuate and often sharply recurved at the periphery. The umbonal region is usually raised and invariably pustulate. Beading in both generations is heavy at the start of the last whorl, less so on later chambers; it may be light, arranged as a single row, in alternating rows or scattered over the surface; it is usually clearly separate from the sutural beads which may be isolated or fused to form bars. Smooth forms are rare.

Cushman (1921) clearly states in his type-description that this species has granulate chamber walls and no sutural beading, but as the type came from a sample containing few specimens, variation in ornament is not discussed. In *O. bartschi* var. *ornata* Cushman (1921) the granules are absent, at least on the later chambers, and only the septa are beaded, while in *O. bartschi* var. *punctata* Yabe & Hanzawa there is beading between the chambers and apparently some on the septa. Hanzawa (1935 : 23) concluded that the varieties of *O. bartschi* probably intergrade, and after consulting Yabe withdrew their varietal name *punctata*, believing, correctly in our opinion, that their specimens were all conspecific with Cushman's type. The affinities of the variety *ornata*, however, remain problematical as it is difficult to differentiate it externally from *Operculina gaymardi* d'Orbigny and *O. complanata* (Defrance), and for this reason it is excluded from our synonymy. For additional information on *O. bartschi* see Cole (1961 : 120).

DISTRIBUTION. *Fossil*: Miocene to Quaternary of the Ryukyu Islands (Yabe & Hanzawa 1925, Hanzawa 1935); Quaternary of the Ryukyus (Yoshiwara 1901) and the New Hebrides (Abrard 1946). *Recent*: Found in the tropical East Indies from the Philippines to Australia.

Subfamily **CYCLOCLYPEINAE** Bütschli, 1880

Genus ***HETEROSTEGINA*** d'Orbigny, 1826

Type-species: *Heterostegina depressa* Parker, Jones & Brady, 1865.

Heterostegina sp.

Pl. 8, figs 9, 10

MATERIAL. 6 specimens. NB 9452.

VARIATION. Length c. 1·00–4·50 mm, width c. 1·00–4·00 mm, thickness c. 0·30–0·40 mm (lowest measurement on broken specimen). Proloculus (internal) diameter 0·08–0·11 mm. Number of chambers in first and second whorls respectively 4½–5 and 9½–12.

Chamber number:	1	2	3	4	5	6	7	8
Number of chamberlets:	undivided		0–2	2–4	3–5	2–3	3–5	3–4

REMARKS. There is heavy beading on the chamber sutures with small beads running parallel to each suture down each chamber as in *H. pusillumbonata* Cole. The chamberlets of the neanic portion, however, are much longer than high, as in *H. operculinoides* Hofker.

Family **HANTKENINIDAE** Cushman, 1927

Subfamily **HASTIGERININAE** Bolli, Loeblich & Tappan, 1957

Genus ***HASTIGERINA*** Thomson *in* Murray, 1876

Type-species: *Hastigerina murrayi* Thomson, 1876 (= *Nonionina pelagica* d'Orbigny, 1839).

Hastigerina siphonifera (d'Orbigny)
Pl. 8, fig. 17

1839 *Globigerina siphonifera* d'Orbigny: 83; pl. 4, figs 15–18.
1960 *Hastigerina* (*Hastigerina*) *siphonifera* (d'Orbigny) Banner & Blow: 22, text-figs 2a–c (lectotype), 3a, b.

MATERIAL. 1 immature specimen. NB 9460.

DIMENSIONS OF FIGURED SPECIMEN. Greatest diameter 0·26 mm, thickness 0·20 mm.

RANGE. Recorded by Blow (1969) as *Hastigerina* (*Hastigerina*) *siphonifera* (d'Orbigny) with an age range of Middle Miocene to Recent (Zone N12–Zone N23).

Family **GLOBIGERINIDAE** Carpenter, Parker & Jones, 1862
Subfamily **GLOBIGERININAE** d'Orbigny, 1826
Genus ***GLOBIGERINA*** d'Orbigny, 1826

Type-species: *Globigerina bulloides* d'Orbigny, 1826.

Plate 10 Thin sections by ordinary transmitted light

Fig. 1 *Pseudomassilina medioelata* sp. nov. P50209. Vertical section. **Paratype,** sample NB 9452. ×50.

Fig. 2 *Pseudomassilina australis* (Cushman). P50210. Vertical section (final chamber broken). Sample NB 9452. ×50.

Fig. 3 *Asterorotalia inspinosa* Huang. P50211. Vertical section. Sample NB 9450. ×60.

Figs 4, 5 *Ammonia togopiensis* sp. nov. Vertical sections. Fig. 1, P50212. Microspheric form (final chamber broken). **Paratype,** sample NB 9452. Fig. 5, P50213. Megalospheric form. **Paratype,** sample NB 9449. Both specimens ×25.

Fig. 6 '*Schackoinella*' *globosa* (Millett). P50214. Vertical section. Sample NB 9447. ×110.

Figs 7–9 *Pseudorotalia indopacifica* (Thalmann). Vertical sections. Fig. 7, P50215. Microspheric form. Sample NB 9460. Fig. 8, P50126. Highly trochoid megalospheric form (trending towards *Rotalia alveiformis* Thalmann). Sample NB 9460. Fig. 9, P50217. Megalospheric form. Sample NB 9449. All specimens ×25.

Figs 10, 11 *Pseudorotalia catilliformis* (Thalmann). Vertical sections. Fig. 10, P50218. Microspheric form (final chamber broken). Sample NB 9456/7. Fig. 11, P50219. Megalospheric form. Sample NB 9454. ×20.

Figs 12, 13 *Pseudorotalia schroeteriana* (Parker & Jones). Vertical sections. Fig. 12, P50220. Immature megalospheric specimen (cf. *Gyroidina conoides* d'Orbigny). Sample NB 9452. ×40. Fig. 13, P50221. Adult megalospheric specimen; the test has outgrown the conical shape. Sample NB 9449. ×30.

Fig. 14 *Calcarina hispida* Brady. P50222. Vertical section. Sample NB 9450. ×40.

Figs 15, 16 *Cellanthus craticulatus* (Fichtel & Moll). P50223, P50224. Equatorial sections of megalospheric and microspheric forms. Sample NB 9452. Fig. 15, ×20; fig. 16, ×12.

Fig. 17 *Epistomaroides polystomelloides* (Parker & Jones). P50225. Off-centre equatorial section. Sample NB 9450. ×40.

Figs 18, 19 *Cellanthus adelaidensis* (Howchin & Parr). P50226, P50227. Equatorial and axial sections. Sample NB 9449. ×20.

Fig. 20 *Elphidiella indopacifica* Germeraad. P50228. Axial section. Sample NB 9449. ×25.

Fig. 21 *Cellanthus biperforatus* sp. nov. P50229. Axial section. **Paratype,** sample NB 9454. ×25.

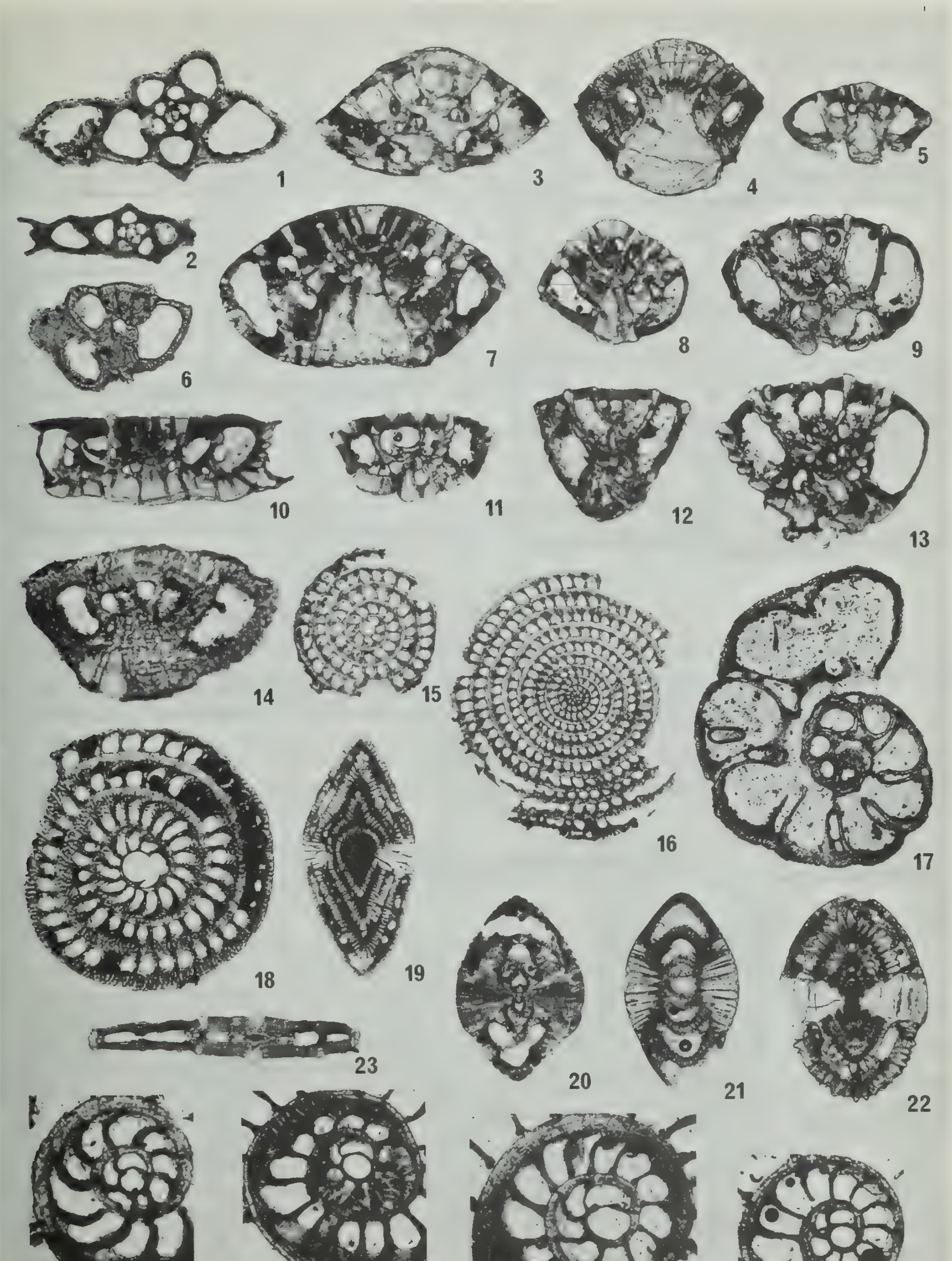
Fig. 22 *Cellanthus hailei* sp. nov. P50230. Axial section; note the poreless plug. **Paratype,** sample NB 9460. ×25.

Figs 23, 27 *Operculina ammonoides* (Schröter). Fig. 23, P50231. Vertical section. Sample NB 9452. ×15. Fig. 27, P50232. Equatorial section, early part of coil. Sample NB 9452. ×40.

Fig. 24 *Operculina bartschi* Cushman. P50233. Equatorial section, early part of coil. Sample NB 9452. ×40.

Fig. 25 *Nummulites tamanensis* (Vaughan & Cole). P50234. Equatorial section, early part of coil. Note characteristic 'trabeculae' in spiral sheet. Sample NB 9452. ×17.

Fig. 26 *Nummulites* cf. *amplicuneatus* (Cole). P50235. Equatorial section, early part of coil. Sample NB 9452. ×40.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Globigerina bulloides d'Orbigny

Pl. 8, fig. 14

1826 *Globigerina bulloides* d'Orbigny : 277, no. 1; modèle 76.
1960a *Globigerina bulloides* d'Orbigny; Banner & Blow : 3; pl. 1, figs 1a–c (lectotype), 4a–c.

MATERIAL. 1 specimen. NB 9450.

DIMENSIONS OF FIGURED SPECIMEN. Greatest diameter 0·20 mm, thickness 0·13 mm.

RANGE. Recorded by Blow (1969) as *Globigerina bulloides bulloides* d'Orbigny with a range of late Miocene to Recent (Zone N16–Zone N23).

Globigerina quinqueloba Natland

Pl. 8, fig. 12

1938 *Globigerina quinqueloba* Natland: 149; pl. 6, fig. 7.

MATERIAL. 5 specimens (mostly with final chamber missing). NB 9447.

DIMENSIONS OF FIGURED SPECIMEN. Greatest diameter 0·20 mm, thickness 0·15 mm.

RANGE. Recorded by Blow (1969) as *Turborotalita quinqueloba* (Natland) with a range of late Miocene to Recent (Zone N17–Zone N23).

Genus *GLOBIGERINOIDES* Cushman, 1927

Type-species: *Globigerina rubra* d'Orbigny *in* de la Sagra, 1839.

Globigerinoides ruber (d'Orbigny)

Pl. 8, fig. 15

1839 *Globigerina rubra* d'Orbigny : 82; pl. 4, figs 12–14.
1960*a* *Globigerina rubra* d'Orbigny; Banner & Blow : 19; pl. 3, figs 8a, b (lectotype).

MATERIAL. 4 immature specimens. NB 9449, 9454.

DIMENSIONS OF FIGURED SPECIMEN. Greatest diameter 0·36 mm, thickness 0·25 mm.

RANGE. Blow (1969) gives the range of *Globigerinoides ruber* (d'Orbigny) as late Miocene to Recent (Zone N16–Zone N23).

Globigerinoides sacculifer (Brady)

Pl. 8, fig. 16

1877 *Globigerina sacculifera* Brady : 535 (description).
1884 *Globigerina sacculifera* Brady; Brady : 604; pl. 80, figs 11–17; pl. 82, fig. 4 (figures).
1960*a* *Globigerina sacculifera* Brady; Banner & Blow : 21; pl. 4, figs 1a, b (lectotype), 2a, b.

MATERIAL. 1 immature specimen. NB 9460.

DIMENSIONS OF FIGURED SPECIMEN. Greatest diameter 0·21 mm, thickness 0·15 mm.

RANGE. Recorded by Blow (1969) as *Globigerinoides quadrilobatus sacculifer* (Brady) *forma typica* (lectotypic form), with a range of early Miocene to Recent (Zone N6–Zone N23).

Subfamily CATAPSYDRACINAE Bolli, Loeblich & Tappan, 1957

Genus *GLOBIGERINITA* Brönnimann, 1951

Type-species: *Globigerinita naparimaensis* Brönnimann, 1951.

Globigerinita glutinata (Egger)

Pl. 8, fig. 13

1893 *Globigerina glutinata* Egger : 371; pl. 13, figs 19–21.

MATERIAL. 9 specimens (characteristic bulla usually broken off). NB 9449.

DIMENSIONS OF FIGURED SPECIMEN. Greatest diameter 0·17 mm, thickness 0·13 mm.

RANGE. Recorded by F. L. Parker (1967) as *Globigerinita glutinata* (Egger) with a range of late Miocene to Recent (Zone N16–Zone N23).

Family **EPONIDIDAE** Hofker, 1951

Genus ***POROEPONIDES*** Cushman, 1944

Type-species: *Rosalina lateralis* Terquem, 1878.

Poroeponides lateralis (Terquem)

Pl. 7, fig. 12

1878 *Rosalina lateralis* Terquem : 25; pl. 7 (2), figs 11a–c.
1884 *Pulvinulina lateralis* (Terquem) Brady : 689; pl. 106, figs 2a–3c.
1915 *Pulvinulina lateralis* (Terquem); Heron-Allen & Earland : 714; pl. 53, figs 6–11.
1921 *Pulvinulina lateralis* (Terquem); Cushman : 336; pl. 69, figs 2a–c.
1949 *Poroeponides lateralis* (Terquem) Said : 36; pl. 4, fig. 3.
1951*d* *Poroeponides lateralis* (Terquem); Asano : 18, text-figs 136, 137.
1956 *Poroeponides lateralis* (Terquem); Bhatia : 23; pl. 3, figs 3, 4, 5a–c.
1959 *Poroeponides lateralis* (Terquem); Graham & Militante : 96; pl. 14, figs 9a–c.
1960 *Poroeponides lateralis* (Terquem); Barker : 218; pl. 106, figs 2a–3c (after Brady).
1961 *Eponides lateralis* (Terquem) Braga : 155; pl. 16, figs 10, 11.
1961 *Poroeponides lateralis* (Terquem); Huang : 87; pl. 4, figs 29, 30.
1964*a* *Poroeponides lateralis* (Terquem); Rocha & Ubaldo : 415; pl. 2, fig. 11.
1965 *Eponides repandus* (Fichtel & Moll); Todd (*pars*) : 20; pl. 7, figs 4a–c only.
1970 *Poroeponides lateralis* (Terquem); Matoba : 58; pl. 8, figs 2a–c.

MATERIAL. 10 specimens. NB 9449, 9450.

VARIATION. Length 0·50–1·50 mm, breadth 0·37–1·12 mm, thickness 0·17–0·60 mm.

REMARKS. Our larger specimens have compressed later-formed chambers embracing the test for over half its circumference with areal pores covering the whole of their ventral surface. The umbilicus is open, sometimes with an umbilical flap.

There are too few well-preserved specimens in the Togopi material for us to follow up Resig's (1962) investigations into the status of the genus *Poroeponides* (see Remarks under *P. cribrorepandus* Asano & Uchio, p. 100).

DISTRIBUTION. *Fossil*: Pliocene of Japan (Asano 1951*d*). The type specimens came from the Pliocene of the Island of Rhodes (Terquem 1878). *Recent*: Has been found in the western Pacific, East Africa, the Red Sea and the west coast of the Indian subcontinent.

Poroeponides cribrorepandus Asano & Uchio

Pl. 7, fig. 11

1951*d* *Poroeponides cribrorepandus* Asano & Uchio *in* Asano : 18, figs 134, 135.
1954 *Poroeponides cribrorepandus* Asano & Uchio; Cushman, Todd & Post : 360; pl. 89, fig. 24.
1955 *Poroeponides cribrorepandus* Asano & Uchio; Takayanagi : pl. 2, figs 19a, b.
1959 *Poroeponides cribrorepandus* Asano & Uchio; Graham & Militante : 96; pl. 14, figs 8a–c.
1963 *Poroeponides cribrorepandus* Asano & Uchio; Matsunaga : pl. 47, figs 3a, b.
1964 *Poroeponides lateralis* (Terquem); Bhatia & Bhalla : pl. 2, figs 3a, b (*non Rosalina lateralis* Terquem, 1878).
? 1964*a* *Eponides repandus* (Fichtel & Moll); Rocha & Ubaldo : 414; pl. 2, figs 10a, b.
1964 *Poroeponides cribrorepandus* Asano & Uchio; Le Roy : F39; pl. 9, figs 26, 27.
? 1964*b* *Poroeponides lateralis* (Terquem); Rocha & Ubaldo : 647 (list); pl. 1, figs 11, ? 15.
1965 *Eponides repandus* (Fichtel & Moll); Moura : 50; pl. 6, fig. 8 (*non Nautilus repandus* Fichtel & Moll, 1798).
? 1968 *Poroeponides lateralis* (Terquem); Bhalla : 387; pl. 2, figs 8a, b.
1970 *Poroeponides cribrorepandus* Asano & Uchio; Kim : pl. 3, figs 2a, b.
1970 *Poroeponides lateralis* (Terquem); Bhalla : 160; pl. 21, figs 6a, b.
1970 *Poroeponides cribrorepandus* Asano & Uchio; Matoba : 58; pl. 8, figs 1a–c.

MATERIAL. 9 specimens, NB 9449, 9450.

VARIATION. Length 0·25–0·77 mm, breadth 0·20–0·60 mm, thickness 0·12–0·37 mm.

REMARKS. The status of *Poroeponides* has been questioned by a number of authors, in particular Resig (1962) who studied the species *Eponides repandus* (Fichtel & Moll) from a Californian offshore sample of Pleistocene age. She states that the early stages were found to be true *Eponides*, but the intermediate stage developed the characters of *Poroeponides cribrorepandus* Asano & Uchio, while the final stages represented forms which have been described as *Sestranophora arnoldi* Loeblich & Tappan.

Loeblich & Tappan (1964 : C684) nevertheless have retained all three genera. They argue that such ontogenetic stages are characteristic of many foraminiferal genera and that only adult stages can be used in classification. We have only the '*Poroeponides*-form' in the Togopi material and therefore cannot comment further.

DISTRIBUTION. *Fossil*: Pliocene of Japan (Asano & Uchio *in* Asano 1951*d*, Matsunaga 1963) and Okinawa (Le Roy 1964). *Recent*: Has been widely reported from the western Pacific, the coasts of India and south-eastern Africa.

Family **AMPHISTEGINIDAE** Cushman, 1927

Genus ***AMPHISTEGINA*** d'Orbigny, 1826

Type-species: *Amphistegina vulgaris* d'Orbigny, 1826.

Amphistegina cf. ***lessonii*** d'Orbigny

Pl. 8, fig. 1

cf. 1826 *Amphistegina lessonii* d'Orbigny : 304, no. 3 (modèle 98 and pl. 17, figs 1–4 probably refer to *A. quoii* d'Orbigny; see Ellis & Messina 1940 *et seqq*.).

MATERIAL. 3 specimens. NB 9449, 9452.

VARIATION. Maximum diameter 1·10 mm, thickness up to 0·60 mm.

REMARKS. Imperfect preservation of our material allows no more than a tentative identification.

Amphistegina cf. ***wanneriana*** Fischer

Pl. 8, fig. 2

cf. 1927 *Amphistegina wanneriana* Fischer; Fischer : 170; pl. 217, figs 131a–c.

MATERIAL. 11 specimens. NB 9450, 9452.

VARIATION. Greatest diameter 0·80–1·70 mm, thickness 0·40–0·70 mm.

REMARKS. *A. wanneriana*, erected by Fischer (1921 : 251) for the *Amphistegina* sp. nov. of Wanner (1910 : 761), was not formally described or figured until 1927 (*op. cit*.).

Our specimens are generally poorly preserved and, therefore, cannot be identified with certainty. They do not have the coarse ornament shown by *A. radiata* (Fichtel & Moll) var. *papillosa* Said or by *A. lessonii* d'Orbigny var. *pulchra* Cushman & Todd.

RANGE. *A. wanneriana* has been recorded only from the Pliocene sediments of eastern Indonesia.

Family **CIBICIDIDAE** Cushman, 1927

Subfamily **CIBICIDINAE** Cushman, 1927

Genus ***CARIBEANELLA*** Bermúdez, 1952

Type-species: *Caribeanella polystoma* Bermúdez, 1952.

Caribeanella ogiensis (Matsunaga)

Fig. 64; Pl. 7, fig. 16

1954 *Oinomikadoina ogiensis* Matsunaga : 163, text-figs 1–3.
1955 *Oinomikadoina ogiensis* Matsunaga; Takayanagi : pl. 2, figs 20a, b.
1963 *Oinomikadoina ogiensis* Matsunaga; Matsunaga : pl. 50, figs 5a–c.

MATERIAL. 20 specimens. NB 9448, 9449, 9450, 9452.

VARIATION. Maximum diameter 0·49–0·70 mm, thickness 0·15–0·27 mm. Number of chambers in final whorl 7–9.

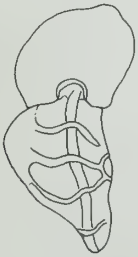


Fig. 64 *Caribeanella ogiensis* (Matsunaga). P50173. Apertural view of specimen figured on Pl. 7, fig. 16. Sample NB 9450. ×65.

REMARKS. Initially like *Cibicides*, this species develops on each of the later-formed chambers of the final whorl two types of supplementary apertures: one, a spiral slit at the inner margin, the other, a smaller aperture at the basal outer margin of the chamber periphery.

Our material agrees closely with the type figures. On the convex ventral surface the sutures are flush or depressed and often marked by a row of coarse pores. On the flattened spiral side the earlier whorls are obscured by thickening of the test; the final whorl has thickened sutures in the early part, narrower and depressed sutures in the later stage. Pores vary in size and distribution, sometimes being sparsely developed. We follow Loeblich & Tappan (1964 : C688–9) in regarding *Oinomikadoina* as a junior synonym of *Caribeanella*.

There is no evidence that *Caribeanella* in the Indo-Pacific is part of the growth cycle of *Planorbulina* as Schnitker (1969) claimed.

DISTRIBUTION. *Fossil*: Pliocene of Japan (Matsunaga 1954, 1963); Matsunaga (1954) also states that the species is found in the Pleistocene of Japan but does not figure the material. *Recent*: Japan (Takayanagi 1955).

Family **PLANORBULINIDAE** Schwager, 1877

Genus ***PLANORBULINELLA*** Cushman, 1927

Type-species: *Planorbulina larvata* Parker & Jones, 1865.

Planorbulinella larvata (Parker & Jones)

Figs 65a, b, 66

1865 *Planorbulina larvata* Parker & Jones : 379, 380; pl. 19, figs 3a, b.
1969 *Planorbulinella larvata* (Parker & Jones) Freudenthal : 82; pl. 4, figs 3, 4; pl. 5, figs 1, 2; pl. 6, fig. 4; pl. 12, figs 4–5b.

MATERIAL. 2 specimens. NB 9448, 9449.

VARIATION. Maximum diameter 0·86–1·36 mm, thickness 0·16–0·32 mm.

DISTRIBUTION. In his comments on the overall distribution of this species Freudenthal (1969) records it as commonly occurring in the Indian and Pacific Oceans (as far north as Japan) and in the Red Sea. There appear to be several reliable records as early as the Miocene (e.g. Le Roy 1964).

Family **ACERVULINIDAE** Schultze, 1854

Genus *GYPSINA* Carter, 1877

Type-species: *Polytrema planum* Carter, 1876.

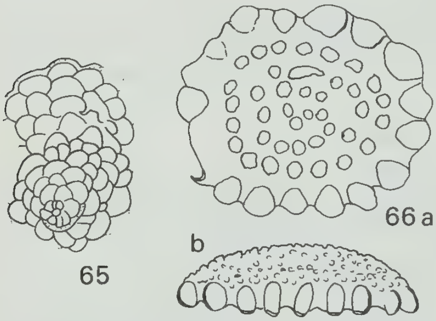
Gypsina globula (Reuss)
Pl. 7, fig. 10

1847 *Ceriopora globulus* Reuss : 33; pl. 5, figs 7a–c.
1884 *Gypsina globulus* (Reuss) Brady : 717; pl. 101, fig. 8.

MATERIAL. 5 specimens. NB 9450, 9452, 9460.

VARIATION. Greatest diameter 0·59–1·83 mm.

RANGE. Miocene (Reuss 1847, Le Roy 1964) to Recent.



Figs 65, 66a, b *Planorbulinella larvata* (Parker & Jones). 65, P50270. Segment of an equatorial half-section. Sample NB 9449. ×30. 66a, b, P50269. Concave side and edge view. Sample NB 9448. ×40.

Family **CYMBALOPORIDAE** Cushman, 1927

Genus *CYMBALOPORETTA* Cushman, 1928

Type-species: *Rosalina squammosa* d'Orbigny *in* de la Sagra, 1839.

Cymbaloporetta squammosa (d'Orbigny)
Pl. 7, fig. 13

1826 *Rotalia squammosa* d'Orbigny : 272 (106), no. 8 (*nomen nudum*).
1839 *Rosalina squammosa* d'Orbigny : 91; pl. 3, figs 12–14.
1839 *Rosalina poeyi* d'Orbigny : 92; pl. 3, figs 18–20.
1884 *Cymbalopora poeyi* (d'Orbigny) Brady : 636; pl. 102, figs 13a–c.
1915 *Cymbalopora poeyi* (d'Orbigny); Cushman : 24; pl. 10, figs 1a–c; pl. 14, figs 5a–c; text-figs 28a–c.
1921 *Cymbalopora poeyi* (d'Orbigny); Cushman : 308; pl. 59, figs 2a–c.
1949 *Cymbaloporetta squammosa* (d'Orbigny) Said : 40; pl. 4, figs 14a, b.
1954 *Cymbaloporetta squammosa* (d'Orbigny); Cushman, Todd & Post : 364; pl. 90, figs 15, 16.
1957 *Cymbaloporetta squammosa* (d'Orbigny); Todd : 292 (table); pl. 91, figs 10a–c.
1959 *Cymbaloporetta squammosa* (d'Orbigny); Graham & Militante : 108; pl. 18, figs 3a–c.
1960 *Cymbaloporetta squammosa* (d'Orbigny); Barker : 210; pl. 102, figs 13a–c (after Brady).
1961 *Cymbaloporetta squammosa* (d'Orbigny); Huang : 88; pl. 4, figs 14, 15.
1964 *Cymbaloporetta squammosa* (d'Orbigny); Rocha & Ubaldo : 144; pl. 17, figs 8, 9, 12.
1965 *Cymbaloporetta squammosa* (d'Orbigny); Todd : 38; pl. 20, figs 3a–c.

MATERIAL. 10 specimens. NB 9449, 9450, 9452.

VARIATION. Maximum diameter 0·52–0·60 mm, height 0·25–0·37 mm. Number of chambers in the last whorl 5–6.

DISTRIBUTION. *Fossil*: Sub-Recent of Timor (Rocha & Ubaldo 1964). *Recent*: Common in the western Pacific islands with an additional record from the Red Sea (Said 1949). First described from the Caribbean.

Cymbaloporetta bradyi (Cushman)

Pl. 7, figs 14, 15

1884 *Cymbalopora poeyi* (d'Orbigny) var.; Brady : 637; pl. 102, figs 14a–d.
1915 *Cymbalopora poeyi* (d'Orbigny) var. *bradyi* Cushman : 25; pl. 10, figs 2a–c; pl. 14, figs 2a–c.
1924 *Cymbalopora bradyi* Cushman; Cushman : 34; pl. 10, figs 2–4.
1932 *Cymbaloporetta bradyi* (Cushman) Thalmann : 310.
? 1941 *Cymbaloporetta poeyi* (d'Orbigny); Le Roy : 42; pl. 3, figs 12–14.
1949 *Cymbaloporetta bradyi* (Cushman); Said : 40; pl. 4, figs 14a, b.
1954 *Cymbaloporetta bradyi* (Cushman); Cushman, Todd & Post : 364; pl. 90, figs 13, 14.
1954 *Cymbaloporetta bradyi* (Cushman); Kleinpell : 68; pl. 9, figs 3a–c.
1957 *Cymbaloporetta bradyi* (Cushman); Todd : 292 (table); pl. 91, figs 12a–c.
1959 *Cymbaloporetta bradyi* (Cushman); Graham & Militante : 108, pl. 18, figs 2a–c.
1960 *Cymbaloporetta bradyi* (Cushman); Barker : 210; pl. 102, figs 14a–d.
? 1961 *Cymbaloporetta bradyi* (Cushman); Huang : 88; pl. 4, fig. 21.
1965 *Cymbaloporetta bradyi* (Cushman); Moura : 54; pl. 7, fig. 3.
1965 *Cymbaloporetta bradyi* (Cushman); Todd : 37; pl. 19, figs 1a–4c; pl. 20, figs 4a–c.
? 1968 *Cymbaloporetta bradyi* (Cushman); Albani : 116; pl. 10, figs 15, 17–19.
1969 *Cymbaloporetta bradyi* (Cushman); Resig : 57; pl. 7, figs 3a, b.
1970 *Cymbaloporetta bradyi* (Cushman); Matoba : 50; pl. 8, figs 7a–c.

MATERIAL. 29 specimens. NB 9449, 9450.

VARIATION. Maximum diameter 0·40–1·2 mm, height up to 0·15 mm. Number of chambers in the last whorl 8–15. Up to eight whorls.

REMARKS. This species shows wide variation in the height of the spire, the number of chambers in the last whorl and in the general shape of the test, probably reflecting the mode of attachment. The umbilicus is usually open, but occasionally it is partially closed by extra shell material. Resig (1969) reports that the '*Tretomphalus*-stage' of the life-cycle has been observed in four of her specimens but no other authors appear to have recorded float-chambers in forms attributable to this species in the Indo-west Pacific region.

For further details of *C. bradyi* see Hofker (1951*b* : 477–484, text-figs 331a–e).

DISTRIBUTION. *Fossil*: Miocene/Pliocene of east Borneo (Le Roy 1941) and Fiji (Kleinpell 1954); Pleistocene of Hawaii (Resig 1969). *Recent*: Widely distributed in the western Pacific with additional records from the Red Sea and south-east Africa.

Cymbaloporetta plana (Cushman)

Pl. 4, figs 19a, b, 20

1924 *Tretomphalus bulloides* (d'Orbigny) var. *plana* Cushman : 36; pl. 10, fig. 8.
1934 *Tretomphalus planus* Cushman; Cushman : 94; pl. 11, figs 11a–c; pl. 12, figs 18–22.
? 1954 *Tretomphalus planus* Cushman; Cushman, Todd & Post : 364; pl. 90, figs 17, 18.
1971 *Tretomphalus bulloides* (d'Orbigny) '*planus* form' Todd : 166.

MATERIAL. '*Tretomphalus* forms' – 4; NB 9449. Specimens without float chamber – 86; NB 9449, 9450.

VARIATION.

	'*Tretomphalus* forms'	Others
Maximum diameter	0·47–0·51 mm	0·29–0·65 mm
Height	0·40 mm	0·15–0·40 mm

Number of chambers in the last whorl 4–7, number of whorls 3–4.

REMARKS. Douglas & Sliter (1965) showed *Tretomphalus* is a junior synonym of *Rosalina*, the float chamber merely characterizing the gamont's planktonic stage. This reproductive phase, moreover, appears to be present in a number of species of *Rosalina* and *Cymbaloporetta*.

In the present material specimens with float chambers are rare, but on dissection are seen to be conspecific with the specimens without 'floats' found in the same sample. The species has the apertural characteristics of *Cymbaloporetta* and a flat or slightly depressed initial coil, and has many fewer chambers than *C. bradyi* (Cushman). It compares most favourably with Cushman's original description of *T. bulloides* var. *plana* (1924 : 36) which states 'the early chambers form a very much flattened cap and the whole "balloon-chamber" [when present] is much wider than high'.

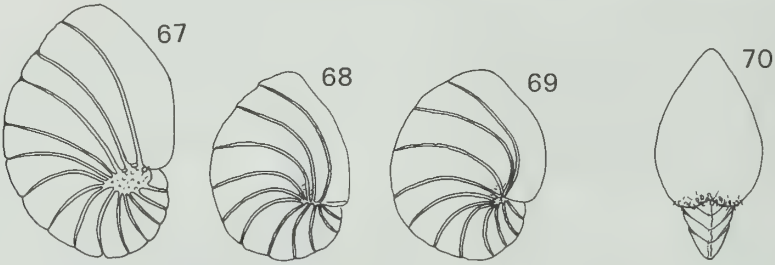
Distribution. From the Recent of Samoa (Cushman 1924, 1934); Guam, Fiji and Pinaki Atoll (Cushman 1934) and possibly Eniwitok (Cushman, Todd & Post 1954). Todd (1971) reports, but does not figure, this form from Midway Atoll, also in the western Pacific. There is no previous fossil record.

Family **NONIONIDAE** Schultze, 1854

Subfamily **NONIONINAE** Schultze, 1854

Genus ***FLORILUS***[4] de Montfort, 1808

Type-species: *Florilus stellatus* de Montfort, 1808, nom. subst. pro *Nautilus asterizans* Fichtel & Moll, 1798.



Figs 67–70 *Florilus asanoi* nom. nov. 67–69, P50271–P50273. Side views showing variation in flaring of test. Sample NB 9450. 70, P50174. Apertural view of specimen figured on Pl. 7, fig. 17. Sample NB 9452. All approx. ×70.

Florilus asanoi nom. nov.

(pro *Nonion japonicum* Asano, 1938)
Figs 67–70; Pl. 7, fig. 17

1933 *Nonion subturgidum* Cushman (*pars*) : 43; pl. 10, figs 7a, b only (*non Nonionina subturgidum* Cushman, 1924).
? 1936*a* *Pseudononion tradecum* Asano : 622; pl. 33, figs 7a–c.
1938*a* *Nonion japonicum* Asano : 593; pl. 15, figs 1–2b.
1941*a* *Nonion boueanum* (d'Orbigny); Le Roy : 78; pl. 1, figs 13, 14 (*non Nonionina boueana* d'Orbigny, 1846).
? 1949 *Nonion nakosoense* Asano : 428, text-fig. 2, nos 14–17.
? 1950 *Nonion kidoharaense iwahorii* Fukuta : 151; pl. 1, figs 2a, b.
1950 *Nonion japonicum* Asano; Asano : 2, text-figs 5, 6.
1959 *Nonion japonicum* Asano; Graham & Militante : 71; pl. 11, fig. 1.
1963 *Nonion japonicum* Asano; Matsunaga : pl. 37, figs 3a, b.
1964 *Nonion japonicum* Asano; Le Roy : F27; pl. 10, figs 12, 13.
1966 *Florilus elongatus* (d'Orbigny); Belford : 158; pl. 31, figs 8–12 (*non Nonionina elongata* d'Orbigny, 1826).
1967 *Nonion japonicum* Asano; Konda : 34 (table); pl. 4, fig. 11.
1968 *Nonion japonicum* Asano; Chiji & Lopez : 108; pl. 15, fig. 6.
1969 *Nonion japonicum* Asano; Konda : 89 (table); pl. 8, fig. 4.

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[4] Since this paper went to press, Dr F. Rögl (personal communication) informs us that an application has been made to the International Commission for Zoological Nomenclature for the suppression of *Florilus*. Following the recent discovery of the Fichtel & Moll Collection in the Natural History Museum, Vienna, Rögl has found that the type-species of *Florilus* de Montfort is in reality a trochospiral form (i.e. a *Hanzawaia*), and therefore, to maintain stability of nomenclature, he considers the generic name should be suppressed, even though it has priority over *Hanzawaia*. If this application is ultimately upheld, the taxonomic position of *F. asanoi* will have to be reviewed.

Material. 196 specimens. NB 9449, 9450, 9452, 9456/7, 9460.

Variation. Length 0·27–0·52 mm, breadth 0·17–0·34 mm, thickness 0·14–0·22 mm. Number of chambers in the final whorl 11–16.

Remarks. Both *Pseudononion japonicum* Asano, 1936 and *Nonion japonicum* Asano, 1938*a*, belong to the genus *Florilus*, and as they are distinct, the latter, which we consider to be conspecific with the present material, must be given a new name. A new name is also necessary if *Florilus* (interpreted by many authors as merely a flaring form of *Nonion*) is not considered to be a true genus. *Pseudononion*, its junior synonym, must then also be rejected, and there would be two species of *Nonion* with the specific name *japonicum*.

The shape of the test in the Togopi specimens is not constant (see Figs 67–69), the coil showing variation from moderately tight to strongly flaring. Nevertheless, the distinctive appearance of the final chamber, when seen in side view, is constant. The umbilicus is granular and the periphery of the shell, characteristically, non-lobate. In edge view the periphery at the beginning of the final whorl is acute to subrounded, and the apertural face variably compressed. *Pseudononion tradecum*, *Nonion kidoharaense iwahorii* and *N. nakosoense*, all from the Neogene of Japan, are very similar to variants in our material and it is possible that they may be conspecific with *Florilus asanoi*.

Florilus asanoi has occasionally been confused with two of d'Orbigny's species from the Tertiary of Europe, *Nonionina boueanum* and *N. elongatus*: *N. boueanum* possesses a markedly lobulate periphery, while *N. elongatus* has a final chamber which is narrow and strongly incurved at the umbilical end instead of broad and embracing as in *F. asanoi.*

Distribution. *Fossil*: ? Miocene (Asano 1949, Fukuta 1950), Pliocene (Asano 1938*a*, Matsunaga 1963) and Pleistocene (Konda 1967, 1969) of Japan; Pliocene of Okinawa (Le Roy 1964) and New Guinea (Belford 1966). Late Tertiary (? Pliocene) of Siberoet Island, Indonesia (Le Roy 1941*a*). *Recent*: The Philippines (Graham & Militante 1959), Japan (Chiji & Lopez 1968) and possibly Fiji (Cushman 1933).

Family **ANOMALINIDAE** Cushman, 1927

Subfamily **ANOMALININAE** Cushman, 1927

Genus ***ANOMALINOIDES*** Brotzen, 1942

Type-species: *Anomalina pinguis* Jennings, 1936.

Anomalinoides glabratus (Cushman)

Figs 71a–c

1924 *Anomalina glabrata* Cushman: 39; pl. 12, figs 5–7.

Material. 2 specimens. NB 9450.

Variation. Length 0·39–0·45 mm, width 0·33–0·34 mm, thickness 0·20 mm.

Remarks. Placed within this genus on apertural characteristics.

Range. Miocene (Matsunaga 1963) to Recent.

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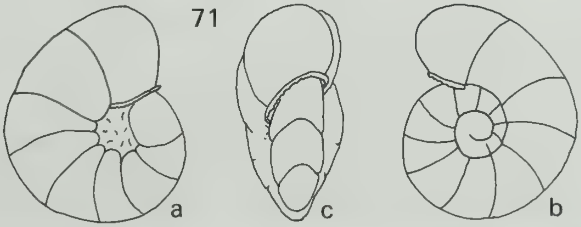

Figs 71a–c *Anomalinoides glabratus* (Cushman). P50274. Ventral, dorsal and apertural views. Sample NB 9450. ×70.

Genus *HANZAWAIA* Asano, 1944

Type-species: *Hanzawaia nipponica* Asano, 1944.

Hanzawaia nipponica Asano
Pl. 7, figs 18a, b

1944 *Hanzawaia nipponica* Asano: 99; pl. 4, figs 1–2b.
1951*c* *Hanzawaia nipponica* Asano; Asano: 16, text-figs 24–26.
1955 *Hanzawaia nipponica* Asano; Takayanagi: 45; pl. 2, figs 21a, b.
1963 *Hanzawaia nipponica* Asano; Matsunaga: pl. 52, figs 5a–c.
1964 *Hanzawaia nipponica* Asano; Ishiwada: pl. 8, figs 113a, b.
1964 *Hanzawaia nipponica* Asano; Le Roy: F46; pl. 9, figs 28, 29.
1967 *Hanzawaia nipponica* Asano; Matoba: 255; pl. 29, figs 14a–c.
1968 *Hanzawaia nipponica* Asano; Chiji & Lopez: 107; pl. 15, figs 14a, b.
1970 *Hanzawaia nipponica* Asano; Kim *et al.*: pl. ix-2, figs 5a–c.
1970 *Hanzawaia nipponica* Asano; Matoba: 55; pl. 8, figs 10a–c.

MATERIAL. 11 specimens. NB 9450.

VARIATION. Length 0·33–0·40 mm, breadth 0·25–0·32 mm, thickness 0·10–0·11 mm.

REMARKS. The Togopi specimens are small for the species and only two show signs of supplementary lobe development, even though all possess clear chamber flaps on the ventral side. Topotypes (BM(NH) no. P45449) from the Kakio Formation of Japan, however, suggest that this feature can be quite variable.

DISTRIBUTION. *Fossil*: Miocene of Okinawa (Le Roy 1964); ? Upper Miocene/Pliocene (Matsunaga 1963), Pliocene (Asano 1944, 1951*c*) and Pleistocene (Matoba 1967) of Japan. *Recent*: Widespread around the coasts of Japan, but elsewhere it appears to have been found only off south-west Korea (Kim *et al.* 1970).

Postscript

Since this paper went to press, Ujiié (1977) has described and figured a number of species he previously listed (1970) from the M. Miocene Sandakan Formation of Sabah. Two of them are of particular reference to the present work as they are stated by us to be extinct and of possible biostratigraphical use (Fig. 3, p. 10).

The first of these, *Bolivina amygdalaeformis* of Ujiié (1977: pl. 5, figs 3a, b), is a *Brizalina* and is referable to Asano's subspecies *Brizalina amygdalaeformis iokensis*, rather than to the nominate subspecies *B. a. amygdalaeformis* (Brady), which never has striations extending onto the last chamber (see p. 55). Ujiié's record is the earliest known occurrence.

The second, *Bolivina* cf. *tikutoensis* Nakamura (Ujiié 1977: pl. 5, figs 7a, b), appears to be very close to or identical with our new taxon *B. sabahensis* (see p. 54), and thus extends its stratigraphical range down into the M. Miocene.

A further postscript is needed concerning the generic assignment of '*Schackoinella*' *globosa* (Millett), p. 63. Quilty (1975: 329) has recently redefined and refigured the poorly-known type-species of *Schackoinella*, *S. sarmatica* Weinhandl from the late Miocene of Austria, and has shown it to be a true glabratellid with an umbilical aperture and radially striate ventral side. Neither the aperture, difficult as it is to discern, nor the ventral appearance of Millett's species would now seem to allow its reference to *Schackoinella*, and therefore we propose to transfer it to *Murrayinella* Farias (1977: 343), a new genus tentatively assigned to the Rotaliidae. *Murrayinella*, type-species *Rotalia murrayi* Heron-Allen & Earland (1915), also includes *R. erinacea* Heron-Allen & Earland, as designated by Farias, which we have synonymized with *Murrayinella globosa* (Millett) (p. 63).

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W. J. Kennedy & H. C. Klinger

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Cretaceous faunas from Zululand and Natal, South Africa. The ammonite family Gaudryceratidae

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Synopsis

Members of the ammonite family Gaudryceratidae occur widely in the South African Cretaceous, and are locally common. The earliest representative of the group, *Eogaudryceras* (*Eogaudryceras*), appears in the Upper Aptian, and species of *Gaudryceras* range to the Campanian. In all, twenty species referred to seven genera have been recognized; thirteen of the species represent new records for the area. The following species are described: *E.* (*Eogaudryceras*) *hertleini* (Wiedmann), *E.* (*E.*) *shimizui* Breistroffer, *Eogaudryceras* (*Eotetragonites*) *raspaili raspaili* Breistroffer, *E.* (*Eotetragonites*) *umbilicostriatus* Collignon, *Gaudryceras* cf. *varagurense* Kossmat, *G. stefaninii* Venzo, *G. varicostatum* van Hoepen, *G. denseplicatum* (Jimbo), *G. tenuiliratum* Yabe, '*Gaudryceras*' *sigcau* van Hoepen, '*Gaudryceras*' spp., *Anagaudryceras buddha* (Forbes), *A. subsacya* (Marshall), *A. politissimum* (Kossmat), *A. subtilineatum* (Kossmat), *A. pulchrum* (Crick), *Vertebrites kayei* (Forbes), *Zelandites odiensis* (Kossmat), *Zelandites* spp., *Kossmatella marut* (Stoliczka) and *Kossmatella* aff. *romana* Wiedmann. Lectotypes of *Anagaudryceras subtilineatum* (Kossmat) and *Vertebrites kayei* (Forbes) are selected. The collections allow illustration of the ontogeny and intraspecific variation in *Anagaudryceras buddha* and *A. pulchrum*, and show *Gaudryceras cinctum* Spath to be a synonym of *G. varicostatum*, '*G.*' *tenuiliratum* van Hoepen to be a synonym of *Anagaudryceras subtilineatum* and *G. amapondense* van Hoepen to be a synonym of *G. denseplicatum*. Several of the species are adequately illustrated for the first time.

Introduction

The superfamily Tetragonitaceae Hyatt, 1900 is a group of long-ranging forms conservative in external morphology, but the most advanced of ammonites in terms of sutures. They have a sexlobate primary suture, with a formula E LU_2 U_3 U_1, and a septal lobe, Is (p. 123). As Wiedmann (1963, 1973) and Kullman & Wiedmann (1970) have demonstrated, this progressive septal pattern suggests that, had the ammonites weathered the Cretaceous/Palaeocene crisis, the tetragonitids would be the group which would probably still be with us. The group evolved from the Lytocerataceae during the Barremian, although no forms with intermediate sutures are known (Wiedmann 1962*a*: 147). There has been considerable disagreement as to the subdivision of the superfamily, and we have adopted Wiedmann's conclusions in dividing the superfamily into two families, the Gaudryceratidae, South African representatives of which are described here, and the Tetragonitidae, to be described subsequently.

The Gaudryceratidae range from Barremian to Maastrichtian, and have a world-wide distribution. They are, however, rare in the boreal areas of north-west Europe and the Soviet Union, and the western interior of North America, being best known from the circum-Pacific area, north, east and west Africa, Madagascar and Antarctica. Typical gaudryceratids (*Gaudryceras*, *Vertebrites*) are evolute, many-whorled, depressed at first, becoming compressed as size increases, with an ornament of coarse to fine lirae, and bearing constrictions. The sutures are typically lytoceratinid, with more or less symmetrical bifid saddles, and a prominent septal lobe. Departures from this type include compressed genera such as *Mesogaudryceras* Spath, 1927 and *Zelandites* Marshall, 1926 or coronate forms with a keel-like lateral angle – *Jaubertella* Jacob, 1908 and *Gabbioceras* Hyatt, 1900.

There have been a number of attempts to subdivide the family. *Kossmatella* Jacob, 1907 has been placed in a subfamily Kossmatellinae Breistroffer, 1953, *Vertebrites* Marshall, 1926 in a subfamily Vertebritinae Wiedmann, 1962 and *Gabbioceras* Hyatt, 1900 and *Jauberticeras* Jacob, 1907 in a subfamily Gabbioceratinae Breistroffer, 1953.

All of the gaudryceratids appear to be intimately related, and species of individual genera often develop, at some stage in ontogeny, features which typify one or other of these subfamilies, as will be clear from our subsequent discussions and those of Wiedmann (1962*a*, *b*), Henderson (1970) and others. We do not, therefore, subdivide the family here.

In South Africa, gaudryceratids first appear in the Upper Aptian, with representatives of *E.* (*Eogaudryceras*). *E.* (*Eogaudryceras*) and *E.* (*Eotetragonites*) occur in the Middle Albian; the Upper Albian yields *Kossmatella* and abundant *Anagaudryceras* at some levels, and we have a few examples of the latter genus from the Upper Cretaceous. *Gaudryceras* appears in the Lower Cenomanian and occurs rarely up to the Campanian.

Most described collections of gaudryceratids consist of relatively few specimens. We have large collections of two species, *Anagaudryceras buddha* and *A. pulchrum*, which allow description of the range of intraspecific variation and ontogenetic changes within the group, whilst redescription of van Hoepen's material (1920, 1921) clarifies the relationships and nomenclatoral problems associated with the five gaudryceratids described by him.

Location of specimens

The following abbreviations are used to indicate the repositories of the material studied:

BM(NH)	British Museum (Natural History), London.
MHNG	Musée d'Histoire Naturelle, Geneva.
EMP	École des Mines, Paris.
MHNP	Muséum d'Histoire Naturelle, Paris.
SAS	South African Geological Survey, Pretoria.
TM	Transvaal Museum, Pretoria.
UND	University of Natal, Durban.
DM	Durban Museum.
SAM	South African Museum, Cape Town.
UPE	University of Pretoria, Pretoria.

Field localities

Outline details of field localities referred to in this paper are given in Kennedy & Klinger (1975); full descriptions of sections are deposited in the Palaeontology Library of the British Museum (Natural History).

Dimensions of specimens

Dimensions of specimens are given below in millimetres; abbreviations are as follows:

D = Diameter
Wb = Whorl breadth
Wh = Whorl height
U = Umbilical diameter

Figures in parentheses are dimensions as a percentage of the total diameter.

Suture terminology

The suture terminology of Wedekind (1916, see Kullman & Wiedmann 1970) is followed in the present work:

Is = Internal lobe with septal lobe
U = Umbilical lobe
L = Lateral lobe
E = External lobe

Systematic palaeontology

Class **CEPHALOPODA** Cuvier, 1797
Subclass **AMMONOIDEA** Zittel, 1884
Order **LYTOCERATIDA** Hyatt, 1899
Superfamily **TETRAGONITACEAE** Hyatt, 1900
Family **GAUDRYCERATIDAE** Spath, 1927

Genus ***EOGAUDRYCERAS*** Spath, 1927

Eogaudryceras is the root stock of all the younger gaudryceratids. Current treatment of the genus is sharply divided between those authors who would restrict it to forms without constrictions (e.g. Spath 1927, Wright 1957, Murphy 1967*a*, *b*) and others (e.g. Wiedmann 1962*a*, *b*) who point to the presence of intermediates between the type species, *E. numidum*, and the type species of *Eotetragonites* Breistroffer, 1947, *E. raspaili* Breistroffer, and divide *Eogaudryceras* into two subgenera. *Eogaudryceras* s. str. gave rise to the gaudryceratids and *E.* (*Eotetragonites*) to the tetragonitids. A further complication arises from the view of Murphy (1967*a*, *b*), who places *Eotetragonites* within the Tetragonitidae because of its phylogenetic position. For our present purposes, we are impressed by Wiedmann's arguments, and have adopted a subdivision of *Eogaudryceras* into subgenera, as described below.

Subgenus ***EOGAUDRYCERAS*** Spath, 1927

TYPE SPECIES. *Ammonites numidus* Coquand 1880 : 22, by original designation.

DIAGNOSIS. Moderately evolute, whorl section initially trapezoidal, becoming rounded and in some cases laterally compressed when adult. Ornament consists of fine, flexuous lirae; mould smooth, constrictions absent or only weakly developed, typically confined to inner whorls. Suture with symmetrically bifid saddles and a large suspensive lobe.

DISCUSSION. *Eogaudryceras* was originally separated from *Eotetragonites* on the basis of the presence of strong constrictions throughout development and a suture with irregularly bifid saddles in the latter genus. Whilst these differences separate the type species, Wiedmann (1962*b* : 35) has pointed to the occurrence of *Eogaudryceras* with constrictions (*E. llosetaense* Breistroffer), *Eotetragonites* without constrictions (*E. blieuxiensis* Breistroffer) or with symmetrical saddles (e.g. Fallot 1920). The two subgenera are thus better separated on the basis of the intially trapezoidal and subsequently rounded whorl and the fine, moderately curved striae of *Eogaudryceras*, as opposed to the square whorl section and general absence of curved striae in *Eotetragonites*. These points stress the similarities and close relationships between the two subgenera, and their critical position in tetragonitid phylogeny.

Eogaudryceras also shows superficial similarities with *Anagaudryceras* Shimizu, 1934, but the fine lirae and frequent collar-ribs and constrictions of that genus differentiate juveniles, whilst adult ornament clearly differentiates the two. *Gaudryceras* Grossouvre, 1894 and *Vertebrites* Marshall, 1926 develop their distinctive ornament at such an early stage that confusion is unlikely.

The following are the chief *Eogaudryceras* (*Eogaudryceras*) species and varieties currently recognized: *Eogaudryceras numidum numidum* (Coquand 1880 : 22) and *E. numidum* (Coquand) *besavoaensis* Collignon (1962 : 13; pl. 221, fig. 956), Aptian-Albian; *E. turgidum* Breistroffer (1947 : 58), Aptian; *E. vocontianum* (Fallot 1920 : 233; pl. 2, fig. 2; text-fig. 4), Albian; *E. muntaneri* Wiedmann (1962*b*: 42; pl. 2, fig. 5; text-fig. 14), Albian; *E. llosetaense* Breistroffer (1947 : 58), Albian; *E. elegans* Basse (1928 : 134; pl. 8, fig. 8; text-figs 11–12), Albian; *E. inequale* Breistroffer (1947 : 58), Albian; *E. shimizui shimizui* Breistroffer (*in* Besairie 1936 : 175–176), Albian; *E. shimizui skoenbergense* Collignon (1949 : 50; pl. 21, figs 2, 3), Albian; *E. shimizui gaonai* Wiedmann (1962*a* : 153; pl. 8, fig. 4; text-fig. 13), Albian; *E. bourritianum bourritianum* (Pictet 1848 : 298; pl. 4, fig. 1a–c), Albian; *E. bourritianum hispanicum* Wiedmann (1962*a* : 155; pl. 12, fig. 6; text-fig. 15), Albian; *E. italicum* Wiedmann & Dieni (1968 : 34; pl. 1, fig. 8; text-fig. 6), Albian; *E. hertleini* (Wiedmann 1962*c* : 16, 18, 19; pl. 1, fig. 3), Aptian.

OCCURRENCE. *E.* (*Eogaudryceras*) ranges from the Upper Aptian to Upper Albian. Species are best known from the western Mediterranean area (southern France, Balearics, Sardinia) but also occur in northern Spain, England, central Europe, north Africa, Madagascar, California and South Africa (Zululand).

Eogaudryceras* (*Eogaudryceras*) *shimizui Breistroffer ***skoenbergense*** Collignon

1949 *Eogaudryceras skoenbergense* Collignon : 50; pl. 21, figs 2, 3.
1960 *Eogaudryceras shimizui* Breistroffer; Casey : 9; pl. 1, fig. 2.
1962*a* *Eogaudryceras shimizui* Breistroffer *skoenbergense* Collignon; Wiedmann : 151 et seqq.
1968 *Eogaudryceras shimizui* Breistroffer *skoenbergense* Collignon; Wiedmann & Dieni : 33 et seqq.

DISCUSSION. Collignon (1949) introduced *Eogaudryceras skoenbergense* in discussions of *E. shimizui*, basing the species on two figured specimens (1949 : pl. 21, figs 2–2b, 3–3b) said to be from the Skoenberg, Zululand. Wiedmann (1962*a* : 151), in his detailed discussion of *Eogaudryceras*, divided *E. shimizui* into three successive subspecies as follows:

High Upper Albian: *Eogaudryceras shimizui gaonai*, with a depressed oval whorl section.
Low Upper Albian: *Eogaudryceras shimizui shimizui*, with a compressed oval whorl section.
Middle Albian: *Eogaudryceras shimizui skoenbergense*, with a rounded whorl section.

Although we have collected no further specimens which can be referred to *E. shimizui skoenbergense*, otherwise than the South African material known only very doubtfully from southern England, comment is needed because of the type locality given for the subspecies. No Middle Albian sediments outcrop on the Skoenberg, and the specimens are therefore of either Upper Albian or Cenomanian age, and *E. shimizui skoenbergense* would thus be the *latest* known *Eogaudryceras*. Alternatively the specimens in fact come from Middle Albian sediments exposed along the Mzinene, well to the west (Kennedy & Klinger 1975), perhaps in the area of our Locality 53, on the farm Izwehelia (1975 : 288).

Eogaudryceras* (*Eogaudryceras*) *hertleini (Wiedmann)

(Pl. 1, fig. 1)

1938 *Lytoceras* (*Gabbioceras*) *wintunium* Anderson : 150 (pars); pl. 15, fig. 5, *non* pl. 16, figs 2–5.
1962*c* *Gabbiocerus hertleini* Wiedmann : 16, 18, 19; pl. 1, fig. 3.
1967*b* *Eogaudryceras hertleini* (Wiedmann) Murphy : 9; pl. 1, figs 2–5.

HOLOTYPE. California Academy of Sciences no. 8767, from the Upper Aptian of Shasta County, California.

MATERIAL. A single specimen, BM(NH) C78755 from the Makatini Formation at Loc. 37, Mzinene River, Zululand (Aptian IV).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb*/*Wh*	*U*
BM(NH) C78755	39·5	18·0 (46)	16·4 (42)	1·1	12·2 (31)

DESCRIPTION. The coiling is relatively involute, over 50% of the previous whorl being covered, with a depressed whorl section (whorl breadth/height ratio varies from 1·2 to 1·1, decreasing as diameter increases) with greatest breadth close to mid-flank. The umbilicus is small, with a subvertical wall and abruptly rounded shoulder. The sides are flattened with a broadly rounded venter during the early growth stages, the whorl section becoming rounded as diameter increases.

The shell surface is covered by fine, flexuous striae which arise at the umbilical seam, and sweep forwards across the ventrolateral shoulders to form a broad, shallow ventral peak. Occasional groups of striae become stronger to produce incipient collar ribs, associated with faint constrictions (Pl. 1, fig. 1a).

The sutures are not fully visible in our specimen, but include a large bifid first lateral saddle (E/L), a smaller bifid second lateral saddle (L/U_2) and a suspensive lobe with a large first auxiliary saddle.

DISCUSSION. Species of *Eogaudryceras* are differentiated chiefly on relative proportions, whorl section, form of growth striae and nature of constrictions, if present. Our specimen thus most closely resembles *Eogaudryceras hertleini*, in particular the specimens figured by Murphy (1967*b* : pl. 1, figs 2–5). These specimens differ, however, in having some well-formed collar ribs, a feature poorly developed in our specimen. Murphy notes some variation in this feature, however, and reference of our material to *E. hertleini* seems acceptable.

Other species can be differentiated from *Eogaudryceras hertleini* as follows. *Eogaudryceras bourritianum bourritianum* (neotype refigured by Wiedmann 1962*a* : pl. 13, figs 2a–b, and by Murphy 1967*b* : pl. 5, fig. 11) has a very depressed whorl section. *E. bourritianum hispanicum* Wiedmann (1962*a* : pl. 12, fig. 6; text-fig. 16) has a depressed, trapezoidal whorl section with a flattened venter. *Eogaudryceras shimizui shimizui*, *skoenbergense* and *gaonai* all have differing whorl sections and are also easily distinguished by the presence of three conspicuous collar-like ribs per whorl. *Eogaudryceras elegans* Basse has a trigonal whorl section and lirae rather than striae; in *E. llosetaense* and *E. muntaneri* there are obvious constrictions, *E. muntaneri* having a trapezoidal whorl section. *E. turgidum* is depressed (whorl breadth/height ratio up to 1·4) with a trapezoidal whorl section. *Eogaudryceras numidum numidum* and *besavoaensis* have differing whorl sections, becoming trigonal and distinctly compressed at large diameters, with an abruptly rounded umbilical shoulder.

OCCURRENCE. *Eogaudryceras hertleini* is known only from the Upper Aptian of California and Zululand.

Subgenus ***EOTETRAGONITES*** Breistroffer, 1947

TYPE SPECIES. *Eotetragonites raspaili* Breistroffer, by original designation.

DIAGNOSIS. Moderately evolute, with a rectangular whorl section, even when young. Shell surface smooth, or finely striate; constrictions typically strong, and present throughout ontogeny. External suture line with asymmetrically bifid saddles; internal suture with an incipient second lateral saddle.

DISCUSSION. The relationship between *Eogaudryceras* and *Eotetragonites* is discussed above. There are also difficulties in separating some *Eotetragonites* from *Tetragonites* species, as might be expected from their phylogenetic relationship. In general, however, the constrictions are deeper in *Eotetragonites* (although unconstricted forms are known) and straight or convex on the flanks with a strong ventral peak. The close relationship of the two taxa remains, however, as is clear from the reference of the same specimen to both in the most recent reviews, one by Wiedmann (1962*b*) and the other by Murphy (1967*a*, *b*).

The chief *Eogaudryceras* (*Eotetragonites*) species are: *E.* (*Eot.*) *raspaili raspaili* Breistroffer (1947 : 47), Aptian; *E.* (*Eot.*) *raspaili jacobi* (Kilian) (*in* Fallot 1920 : 237; pl. 2, fig. 7; text-fig. 6), Aptian; *E.* (*Eot.*) *jallabertianus* (Pictet 1848 : 302; pl. 4, figs 2a–b), Albian; *E.* (*Eot.*) *plurisulcatus* Breistroffer (1947 : 57), Aptian; *E.* (*Eot.*) *umbilicostriatus* Collignon (1949 : 48; pl. 13, figs 4a–b; pl. 21, fig. 5), Albian; *E.* (*Eot.*) *duvalianum duvalianum* (d'Orbigny 1841 : 158; pl. 50, figs 4–6), Aptian; *E.* (*Eot.*) *duvalianum* (d'Orbigny) *cheinourense* Breistroffer & Mahmoud (1956 : 81), Aptian-Albian; *E.* (*Eot.*) *kossmatelliformis* (Fallot 1920 : 240; pl. 2, figs 4a–c), Aptian; *E.* (*Eot.*) *gainesi* (Anderson 1938 : 153; pl. 20, figs 3, 4, 5), Albian; *E.* (*Eot.*) *wintunius* (Anderson 1938 : 150; pl. 16, figs 2–5, *non* pl. 15, fig. 5, = *Eogaudryceras hertleini* (Wiedmann)), Aptian; *E.* (*Eot.*) *shoupi* Murphy (1967*b* : 22; pl. 3, figs 7, 8, 9), Aptian; *E.* (*Eot.*) *crudus* Drushchits (1956 : 105; pl. 8, fig. 29), Lower Albian; *E.* (*Eot.*) *gardneri* Murphy (1967*a* : 75; pl. 1, figs 6–9), Aptian.

OCCURRENCE. *Eotetragonites* ranges from the Upper Aptian to Middle Albian. Species are best known from the western Mediterranean (southern France, Balearics), and also occur in central Europe, Bulgaria, the Caucasus, north Africa, South Africa (Zululand), Madagascar and California.

Eogaudryceras* (*Eotetragonites*) *raspaili raspaili Breistroffer
(Pl. 1, fig. 6)

1866 *Ammonites depressus* Raspail : 29; pl. 2, fig. 9 (non *Ammonites depressus* Bruguière 1789).
1913 *Lytoceras* (*Tetragonites*) *depressus* (Raspail) Kilian : 329; pl. 11, fig. 3a–b.
1920 *Tetragonites depressus* (Raspail); Fallot : 239; pl. 2, fig. 8; text-fig. 7.
1947 *Eotetragonites depressus* (Raspail) Breistroffer : 56.
1947 *Eotetragonites raspaili* Breistroffer : 83.
1962*b* *E.* (*Eotetragonites*) *raspaili* Breistroffer; Wiedmann : 44.

HOLOTYPE. Original of *Lytoceras* (*Tetragonites*) *depressus* (Raspail) Kilian (1913 : 329; pl. 11, fig. 3), from the Aptian of southern France.

MATERIAL. One specimen only, BM(NH) C78772 from the Mzinene Formation at Loc. 175, Ndumu, Zululand (Albian III).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
BM(NH) C78772	30·0	–	10·8 (36)	–	11·5 (38)

DESCRIPTION. The coiling is moderately evolute, slowly expanding, and distinctly polygonal on the outer whorl. The umbilicus is of moderate size (26% of diameter), shallow, with an outward-sloping wall and an abruptly rounded shoulder. The flanks are flattened and subparallel, the ventrolateral shoulders abruptly rounded, and the venter flattened. The surface of the shell is virtually smooth, save for fine, straight prorsiradiate striae on the flanks, which flex forwards across the ventrolateral shoulders to form a broad ventral peak. There are eight constrictions on the outer whorl; these are shallow on the shell, but deep and prominent on the internal mould, which is otherwise smooth. Constrictions arise at the umbilical seam, are strongly prorsiradiate on the flank, straight at first, but becoming faintly convex as diameter increases. They pass straight up the umbilical wall, sweep forwards across the inner flank and are markedly prorsiradiate, flex backwards across the mid-flank to pass straight across the upper flank, faintly backwards across the ventrolateral shoulder and forwards across the venter to form a very shallow, broad ventral peak. Occasional striae are strengthened into low ribs (?3 on the outer whorl), perhaps corresponding to the constrictions on the internal mould.

The suture includes a large assymetrically bifid first lateral saddle (E/L) and a smaller but otherwise similar second lateral saddle (L/U_2) separated by a large, deeply incised, bifid lateral lobe (L).

DISCUSSION. The limited number of constrictions on our specimen, their course, at first straight but later slightly convex, and the rectangular whorl section compare well with published figures of *Eotetragonites raspaili*. The rounded ventrolateral shoulders further suggest our specimen is closer to the restricted form than to *Eotetragonites raspaili jacobi*, where the shoulders are markedly angular.

Other species, including *Eotetragonites jallabertianus* (see Murphy 1967*b*: pl. 5, figs 7–8 for photographs of the type material), *E. plurisulcatus* (= *Tetragonites duvali* Anthula 1899: pl. 7, figs 3a–b), *E. duvalianum duvalianum* and *cheinourense*, *E. kossmatelliformis*, *E. umbilicostriatus*, *E. gainesi*, *E. shoupi* and *E. wintunius* all have far more constrictions, and these are generally curved or flexuous.

OCCURRENCE. Upper Aptian of the western Mediterranean; Middle Albian of Zululand.

Eogaudryceras (*Eotetragonites*) *umbilicostriatus* Collignon
(Pl. 1, fig. 3)

1949 *Eotetragonites umbilicostriatus* Collignon: 48; pl. 8, fig. 4; pl. 21, fig. 5.
1963 *Eotetragonites umbilicostriatus* Collignon; Collignon: 17; pl. 248, fig. 1060.

HOLOTYPE. Original specimen figured by Collignon (1949: pl. 8, fig. 4; pl. 21, fig. 5) from the Lower Albian of Ambarimaninga, Madagascar.

MATERIAL. A single specimen, BM(NH) C78830 from the Mzinene Formation at Loc. 36 on the Mzinene River, Zululand (Albian III).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
Holotype (from Collignon 1949: 48)	21·0	9 (43)	8 (38)	1·13	8 (38)
Collignon 1963: 17	71·0	32 (45)	32 (42)	1·00	25 (35)
BM(NH) C78830	38·0	–	14·6 (38)	–	15·2 (40)

DESCRIPTION. The specimen is poorly preserved, one side being abraded; it retains recrystallized test, so the sutures are not visible although the specimen is wholly septate. The coiling is fairly evolute, the whorls expanding at a moderate rate, with a ? depressed subrectangular whorl section, the greatest breadth being close to mid-flank. The umbilicus is broad and shallow, with a rounded, outward-sloping wall and an abruptly rounded shoulder. The sides are flattened and subparallel, the ventrolateral shoulder rounded, and the venter flattened. The test is weathered, and growth striae, if once present, are no longer preserved. Instead, there are closely-spaced shallow, flexuous constrictions on the outer whorl. These arise at the umbilical seam, pass straight up the umbilical wall, flex gently forwards and are slightly convex on the flanks, flex gently backwards across the upper flank, and gently forwards across the shoulder to connect across the venter with a weak ventral peak.

So far as can be seen, the inner whorls bore fewer, broader, straighter constrictions, ? 6 per whorl.

Discussion. Collignon (1949) based *Eotetragonites umbilicostriatus* on a juvenile specimen with four to five strong constrictions and a curious umbilical ornament. Subsequently (1963 : 17; pl. 248, fig. 1060) he figured an adult showing denser constrictions, with which our specimen closely agrees.

Eotetragonites umbilicostriatus can be separated from other species of the subgenus on the basis of the curious juvenile ornament, but when this is not preserved, the closely-spaced constrictions are diagnostic, being far less flexed than those of *Eotetragonites duvalianum*, *E. plurisulcatus*, *E. wintunius* or *E. gardneri*. The constrictions of *E. balmensis* are straight on the flank, and the proportions are quite different; adult *E. jacobi* and *E. blieuxiensis* lack prominent constrictions, *E. raspaili* has far fewer constrictions and a squarer whorl section, whilst the poorly-known *E. jallabertianus* has rather more, flexuous constrictions.

Occurrence. Lower Albian of Madagascar and South Africa (Zululand).

Genus *GAUDRYCERAS* de Grossouvre, 1894

Type species. *Ammonites mitis* von Hauer, 1866, by the subsequent designation of Boule, Lemoine & Thévenin (1906).

Synonymy. *Epigaudryceras* Shimizu, 1934 (type species *Gaudryceras striatum* Jimbo 1894, by original designation); *Pseudogaudryceras* Shimizu, 1934 (type species *Gaudryceras tenuiliratum* var. *infrequens* Yabe 1903, by original designation); *Hemigaudryceras* Shimizu, 1934 (type species *Lytoceras* (*Gaudryceras*) *denmanense* Whiteaves 1901, by original designation); *Neogaudryceras* Shimizu, 1934 (type species *Gaudryceras tenuiliratum* Yabe 1903, by original designation).

Diagnosis. Typically evolute, early whorls depressed, slowly expanding, later whorls compressed, expanding more rapidly. Ornament consists of lirae, flexuous or branched, fine and wire-like throughout ontogeny or coarsening and bunching on the outer whorl. Constrictions are present on the internal mould, being marked on the shell by faint collars and depressions. Suture with large bifid lobes and saddles, suspensive lobe typically retracted, with several auxiliaries.

Discussion. This genus has been reviewed at some length by Wright & Matsumoto (1954 : 111–113), Matsumoto (1959*a* : 141) and Howarth (1965 : 360). Wiedmann (1962*a* : 156) provides a detailed synonymy for the genus, but we feel that, given currently accepted generic divisions of the gaudryceratids, *Anagaudryceras* Shimizu, 1934 and *Mesogaudryceras* Spath, 1927 bear separation as either genera or subgenera.

About thirty specific names have been given to gaudryceratids which can be placed in the genus with certainty, as listed by Collignon (1956 : 67–69) and Howarth (1965 : 360), to which can be added *Gaudryceras anomatum* Collignon 1966 and *Gaudryceras yokoyamaiforme* Collignon 1969.

Species of the genus fall into three subgroups, which may be differentiated on characters of adult ornamentation. They probably do not merit subgeneric separation:

1. The group of *Gaudryceras mite* von Hauer, where fine, equal ribs are present throughout ontogeny. The chief species are: *Gaudryceras mite* von Hauer (1866 : 6; pl. 2, figs 3, 4), Santonian to Campanian; *Gaudryceras varagurense* Kossmat (1895 : 122; pl. 17, fig. 9; pl. 18, fig. 2) Turonian to Campanian; *Gaudryceras analabense* Collignon (1956 : 54; pl. 6, figs 1–3), Coniacian; *Gaudryceras beantalyense* Collignon (1956 : 53; pl. 5, figs 1–3), Coniacian; *Gaudryceras varicostatum* van Hoepen (1921 : 7; pl. 2, figs 10–12); *Gaudryceras devallense* Anderson (1958 : 183; pl. 41, fig. 4), Coniacian or Santonian; *Gaudryceras striatum* Jimbo (1894 : 181; pl. 6, fig. 6), Santonian to Maastrichtian; *Gaudryceras stefanini* Venzo (1936 : 21; pl. 2, figs 3, 4), Cenomanian.

2. The group of *Gaudryceras denseplicatum* Jimbo, in which coarse, fold-like ribs appear in the adult in addition to finer lirae (= *Neogaudryceras* Shimizu, 1934). The chief species are: *Gaudryceras denseplicatum* (Jimbo 1894 : 182; pl. 23, figs 1–1a), Turonian to Campanian; *Gaudryceras glannegense* Redtenbacher (1873 : 119; pl. 27, figs 3a–b), Coniacian; *Gaudryceras lauteli* Collignon (1956 : 57; pl. 7, figs 1–1a), Santonian; *Gaudryceras vascogoticum* Wiedmann (1962*a* : 159; pl. 9, figs 2, 6; text-fig. 17), Coniacian; *Gaudryceras amapondense* van Hoepen (1920 : 142; pl. 24, figs 1–3), Santonian to Campanian.

3. The group of *Gaudryceras tenuiliratum* Yabe with finely ribbed inner and coarsely ribbed outer whorls. This includes *Gaudryceras tenuiliratum* Yabe (1903 : 19; pl. 3, figs 3, 4), Coniacian to Campanian; and *Gaudryceras denmanense* Whiteaves (1903 : 329), Campanian.

In addition there is almost a score of juvenile gaudryceratids described in the literature which may be valid species or mere inner whorls of well-known forms. Many of these are listed by Collignon (1956 : 70).

Gaudryceras is readily separable from the more closely related gaudryceratid genera as follows. *Anagaudryceras* Shimizu, 1934, is typically very finely lirate, with widely-spaced constrictions and collars when young, and has adult whorls which may or may not develop coarse folds (= *Paragaudryceras* auctt.) by approximation of constrictions. *Mesogaudryceras* Spath, 1927, is compressed, involute, and finely lirate, without constrictions. *Vertebrites* Marshall, 1926, is small, very evolute, serpenticone, with depressed whorls and an ornament of strong lirae on the flank which split into hair-like striae over the venter. Some *Gaudryceras* (e.g. *G. stefaninii*) develop this feature when young, foreshadowing the persistence of the feature in adult *Vertebrites*.

OCCURRENCE. *Gaudryceras* has a time range extending from Upper Albian to Maastrichtian; the geographical range includes Antarctica, New Zealand, Madagascar, South Africa (Zululand and Natal), Angola, north Africa, the Middle East, central and southern Europe, southern India, Japan, Sakhalin, Kamchatka, Alaska, British Columbia, California, Chile and southern Patagonia.

***Gaudryceras* cf. *varagurense* Kossmat**
(Pl. 1, figs 4, 7)

cf. 1895 *Lytoceras* (*Gaudryceras*) *varagurense* Kossmat : 122; pl. 17, fig. 9; pl. 18, figs 2a–c.
cf. 1965 *Gaudryceras varagurense* Kossmat; Howarth : 36; pl. 4, fig. 5; pl. 5, figs 1–2 (with synonymy).
cf. 1965*a* *Gaudryceras varagurense* Kossmat; Collignon : 2; pl. 376, fig. 1635.
cf. 1965*b* *Gaudryceras varagurense* Kossmat; Collignon : 2; pl. 415, fig. 1712.
cf. 1966 *Gaudryceras varagurense* Kossmat; Collignon : 2, 3; pl. 455, fig. 1852.
cf. 1966 *Gaudryceras varagurense* Kossmat; Howarth : 4; pl. 1, figs 6, 7 (with synonymy).

MATERIAL. Two specimens. SAS SM/2 from the St Lucia Formation at Loc. 63, Skoenberg, Zululand (Coniacian I); BM(NH) C78825 from the St Lucia Formation at Loc. 85, False Bay (Santonian I).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
SAS SM/2	31·8	11·6 (36)	10·8 (34)	1·07	15·6 (49)

DESCRIPTION. The smaller specimen, SAS SM/2, is wholly septate, and retains recrystallized test. The coiling is very evolute, the whorls slowly expanding, depressed, but becoming less so as diameter increases. The greatest breadth is some way below mid-flank. The umbilicus is broad and shallow, with a low, subvertical wall, abruptly rounded shoulder, somewhat flattened, rounded, convergent flanks and a broad, arched venter.

Ornament consists of fine dense lirae, which typically arise at all points from the umbilical seam to mid-flank; many branch at various points on the flank. The lirae pass forwards across the umbilical wall, are markedly prorsiradiate on the lower flank, but flex backwards at mid-flank only to flex forwards across the ventrolateral shoulder to form a distinct if shallow ventral peak. There are ? six strong collar-like ribs on the outer whorl, preceding shallow, narrow constrictions. The sutures are not visible.

The larger specimen, BM(NH) C78825, is a mere fragment, with a maximum whorl height of

18 mm. At this size, the whorls appear to have been slightly compressed, with convergent flanks. Typical flexuous lirae are present on the test, but the internal mould is smooth, save for constrictions. The suture line is poorly exposed, but includes an asymmetrically bifid first lateral saddle (E/L), a smaller second lateral saddle (L/U_2) and a weakly retracted suspensive lobe.

DISCUSSION. The dense, even lirae and relative proportions of our two specimens clearly place them in the group of *Gaudryceras varagurense*; the ornament of our smaller specimen matches closely the inner whorls of Kossmat's type.

The taxonomy of this species has been clarified by Howarth (1965 : 362). As he notes, *Gaudryceras mite* is too poorly understood at present for satisfactory interpretation, whilst there are three names applied to forms matching our material in the Indian Ocean area: *G. varagurense* known from Cenomanian to Campanian, and *Gaudryceras analabense* and *G. beantalyense* both from the Coniacian of Madagascar, where they occur with *G. varagurense*. From the published figures, we doubt, however, that these species bear separation, although our material does not allow comment on the problem. *G. analabense* is said to possess markedly flexuous fine lirae with a strong ventral projection; *G. beantalyense* has less flexuous lirae and lacks a projection.

OCCURRENCE. *Gaudryceras varagurense* ranges from Turonian to Campanian, and there are records from Spain, southern India, Madagascar, Antarctica and Angola in addition to our present Zululand occurrences.

Gaudryceras stefaninii Venzo
(Pl. 1, figs 2, 5, 8; Pl. 2)

1936 *Lytoceras* (*Gaudryceras*) *stefaninii* Venzo : 21; pl. 2, figs 3, 4.
1956 *Gaudryceras stefaninii* Venzo; Collignon : 67.
1963 *Gaudryceras stefaninii* Venzo; Collignon : 16; pl. 247, fig. 1057.
1964 *Gaudryceras stefaninii* Venzo; Collignon : 4; pl. 318, fig. 1352.

TYPE. In a letter dated 15.5.1974, Dr Ladini Walter of the Museo di Paleontologica of the University of Pisa informed us that part or all of Venzo's collection may have been destroyed during the 1939–45 war. We have therefore refrained from designating a lectotype, since neotype designation may be necessary when the condition of the Venzo collection is known.

MATERIAL. Eight specimens, all from the Lower to Middle Cenomanian, Mzinene Formation of Loc. 62, Skoenberg, Zululand: SAS A834, SM/1, A1086; BM(NH) C78758–61, C78765.

Plate 1 × 1, except Figs 2d–e

Fig. 1 *Eogaudryceras* (*Eogaudryceras*) *hertleini* (Wiedmann). BM(NH) C78755, Makatini Formation, Aptian IV, Loc. 37, on Mzinene River, Zululand.

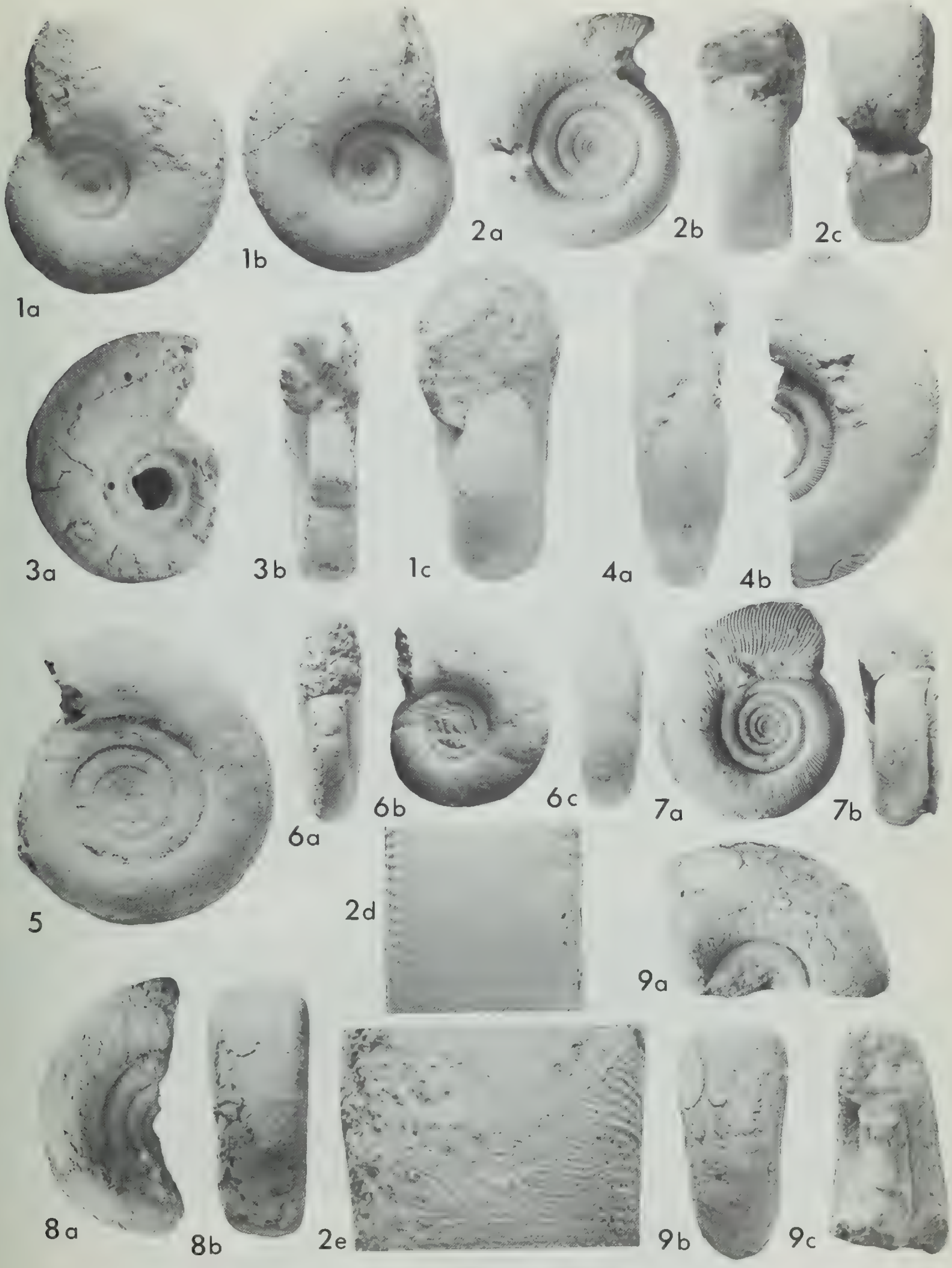
Figs 2, 5, 8 *Gaudryceras stefaninii* Venzo. Fig. 2, SAS A834, Figs 2d–e × 3 to show details of ribbing on venter; Fig. 5, BM(NH) C78759; Fig. 8, SAS SM/1; all Lower to Middle Cenomanian Mzinene Formation at Loc. 62, the Skoenberg, Zululand. See also Plate 2.

Fig. 3 *Eogaudryceras* (*Eotetragonites*) *umbilicostriatus* Collignon. BM(NH) C78830, Mzinene Formation, Albian III, Loc. 36, Mzinene River, Zululand.

Figs 4, 7 *Gaudryceras* cf. *varagurense* Kossmat. Fig. 4, BM(NH) C78825, St Lucia Formation, Santonian 1, Loc. 85, False Bay, Zululand; Fig. 7, SAS SM/2, St Lucia Formation, Coniacian I, Loc. 63, the Skoenberg, Zululand.

Fig. 6 *Eotetragonites* (*Eotetragonites*) *raspaili raspaili* Breistroffer. BM(NH) C78772, Mzinene Formation, Albian III, Loc. 175, Ndumu, Zululand.

Fig. 9 *Anagaudryceras* aff. *sacya* (Crick) (*non* Forbes). BM(NH) C18140, figd Crick (1907*a* : pl. 10, fig. 13), Mzinene Formation, presumably Albian or Cenomanian, Skoenberg area, Zululand. See p. 148.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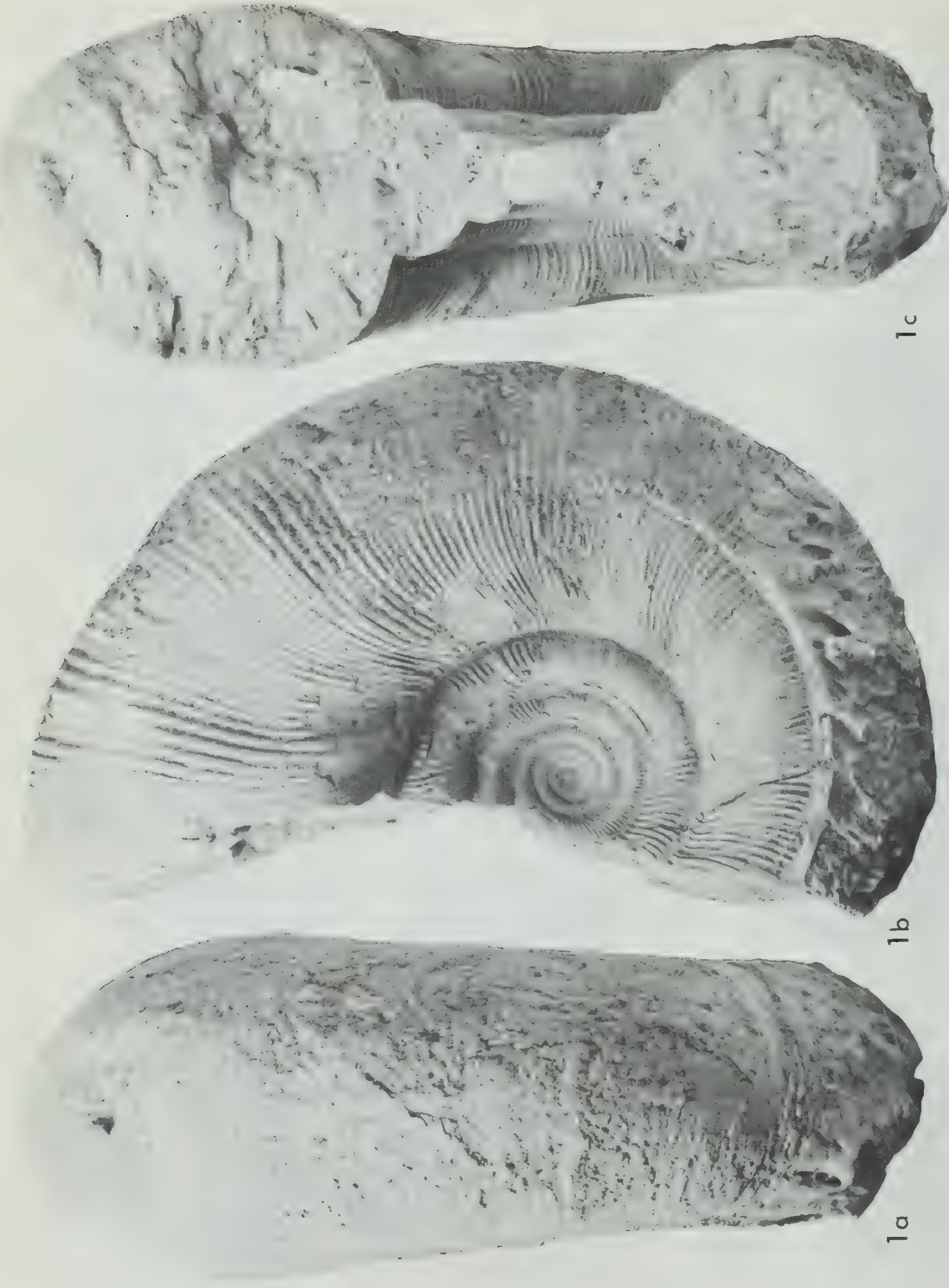

Plate 2
Gaudryceras stefaninii Venzo. SAS A1086, Mzinene Formation, Lower or Middle Cenomanian, Loc. 62, the Skoenberg, Zululand. See also Pl. 1, figs 2, 5, 8.

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
Syntype (Venzo 1936)	29	12 (41)	9 (31)	1·33	15 (51)
Collignon, 1963 : pl. 247, fig. 1057	19·0	80 (42)	60 (32)	1·33	90 (47)
SAS A834	34·5	14·6 (42)	9·5 (28)	1·53	17·2 (50)
SAS SM/1	36·2	14·9 (41)	10·1 (28)	1·47	17·4 ? (48)
BM(NH) C78759	43·8	16·1 (37)	12·3 (28)	1·30	22·9 (52)
SAS A1086	c. 120	50·3 (41)	52·8 (44)	0·95	43·0 (36)

DESCRIPTION. *Early whorls, up to 35 mm.* The coiling is very evolute, serpenticone, the whorls slowly expanding, the whorl section very depressed (whorl breadth/whorl height ratio up to 1·53). The umbilicus is broad, shallow, with a low outward-sloping umbilical wall. The sides are strongly curved, with the greatest breadth at mid-flank. The ventrolateral shoulder is abruptly rounded, the venter flattened. Fine, dense, subequal lirae arise at the umbilical seam, sweep gently forwards across the umbilical wall, shoulder and flanks, sometimes branching low on the flank, at which point intercalated ribs may also appear. At the ventrolateral shoulder, lirae break up into bundles of extremely fine striae in *Vertebrites*-like fashion (Pl. 1, figs 2d–e), and pass straight across the venter. There are occasional straight, prorsiradiate, shallow, narrow constrictions.

35–60 mm. The expansion rate increases, the whorls become progressively less depressed, and eventually as broad as high. The umbilicus becomes smaller, and somewhat deeper. The lirae progressively coarsen, sweep forwards over the umbilical shoulder but are flexed on the lower flank, then pass straight across the upper flank and venter. Some branch, and occasional intercalated lirae appear low on the flank. Periodic prorsiradiate constrictions are present, becoming increasingly closely spaced as diameter increases; behind each is a thickened, collar-like rib, also bearing lirae. When visible, the venter shows that lirae at first divide into twos and threes, but eventually pass across the venter without division.

60–120 mm. The expansion rate increases, so that the umbilicus becomes progressively smaller and deeper. Whorl height increases, and at the largest diameter preserved, the whorl is laterally compressed. Lirae coarsen, and collar-like ribs, bearing lirae, become frequent (Pl. 2, figs 1a–b); in other respects, the ornament is like that of the middle growth stages.

The sutures are not fully exposed.

DISCUSSION. Our collections provide the first detailed ontogenetic series for this curious species; our largest specimen is still wholly septate at 120 mm, and bears traces of a further septate half whorl.

The depressed early whorls, with straight lirae on the flank and *Vertebrites*-like branching over the venter, readily separate this species from *Gaudryceras varagurense*, *G. beantalyense*, *G. analabense* and *G. multiplexum* at comparable diameters.

Gaudryceras vertebratum Kossmat (1895 : 126; pl. 15, figs 4–5) has inner whorls which are depressed like those of *G. stefaninii*, show a flattened venter, straight prorsiradiate lirae on the flank and a 'smooth' venter, but the outer whorl shows finer lirae than in our specimens. Without further Indian material it is not possible to assess the significance of these minor differences, or to place *stefaninii* in synonymy with *vertebratum*; the two species thus stand in the same relationship to each other as *Gaudryceras varagurense* does to *G. analabense*.

Gaudryceras isovokyense Collignon (1964 : 31; pl. 324, fig. 1447) is a further Cenomanian species with a similar whorl section to *G. stefaninii*. The ribs do not, however, develop fine branches over the venter so far as can be seen from the figure, but this may reflect no more than slightly different rates of ontogenetic change.

OCCURRENCE. Lower and Middle Cenomanian of Zululand, Albian and Lower Cenomanian of Madagascar.

Gaudryceras varicostatum van Hoepen

(Fig. 1; Pl. 3, figs 1–3; Pl. 4; Pl. 7, fig. 2; Pl. 14, fig. 11)

1921 *Gaudryceras varicostatum* van Hoepen: 7; pl. 2, figs 10–12; text-figs 3, 4.
1921*b* *Gaudryceras kayei* (Forbes); Spath : 50 (table).

1922 *Gaudryceras varicostatum* van Hoepen; Spath : 117.
1922 *Gaudryceras cinctum* (Crick ms) Spath : 118; pl. 9, figs 3a–3b.
? 1926 *Gaudryceras propemite* Marshall : 142; pl. 20, fig. 4; pl. 28, figs 3, 4.
1931 *Lytoceras* (*Gaudryceras*) *varicostatum* (van Hoepen); Collignon : 12; pl. 2, figs 1–4; pl. 8, fig. 3.
1956 *Gaudryceras* sp. aff. *cinctum* (Crick) Spath; Collignon : 55; pl. 5, figs 4, 5.
1956 *Gaudryceras varicostatum* van Hoepen; Collignon : 56.
1965 *Gaudryceras varicostatum* van Hoepen; Howarth : 362.
1965 *Gaudryceras cinctum* Spath; Howarth : 362.
1966 *Gaudryceras varicostatum* van Hoepen; Collignon : 3; pl. 456, fig. 1854.
? 1970 *Gaudryceras propemite* Marshall; Henderson : 15; pl. 2, fig. 6.

HOLOTYPE. By monotypy, TM 538, the original of van Hoepen 1921 : 7; pl. 2, figs 10–12, from the Umzamba Formation, Loc. 1, Pondoland (Santonian to Campanian).

MATERIAL. Five specimens. The holotype TM 538, SAS P1418 and the holotype of *Gaudryceras cinctum* BM(NH) C19415, all from the late Santonian to early Campanian, Umzamba Formation, at Loc. 1, the mouth of the Umzamba River, southern Natal (Pondoland). SAS Z999 from the St Lucia Formation at Loc. 93 on the farm Ncedomhlope, ESE of Hluhluwe, Zululand (Coniacian II). SAS FB11 from the St Lucia Formation in the southern part of False Bay (age unknown). SAS Z1157 from the St Lucia Formation (Campanian II) the Nibela, Lake St Lucia, Zululand.

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
TM 538	39·6	14·7 (37)	13·7 (35)	1·07	17·2 (43)
BM(NH) C19415 (a)	65·3	–	25·3 (38)	–	22·3 (34)
(b)	49·0	18·2 (37)	17·2 (35)	1·1	18·5 (37)
SAS P1418	29·3	10·7 (36)	9·8 (33)	1·09	14·0 (47)

DESCRIPTION. *Early whorls, up to 40 mm* (Pl. 3, figs 1–3). The coiling is evolute, slowly expanding, with a depressed whorl section (whorl breadth/height ratio 1·1), the greatest breadth being close to the umbilicus. The whorl sides and venter are rounded, the latter being a little flattened. The umbilicus is broad and of moderate depth, with a rounded wall and abruptly rounded shoulder. Fine, dense, prorsiradiate flexuous lirae arise at the umbilical seam, sweep forwards across the shoulder and inner flanks, and gently backwards across mid-flank. A few lirae branch at the umbilicus and some intercalate on the flanks. The ventrolateral shoulders and venter are covered in fine dense striae, invisible to the naked eye, and produced by the splitting of the lirae at a position corresponding approximately to the umbilical seam of the succeeding whorl (Pl. 3, figs 3c–d). Occasional strengthened collar-like ribs are present on the test, corresponding to the site of shallow constrictions on the otherwise smooth internal mould.

Middle and later growth stages (Pl. 3, fig. 2; Pl. 4; Pl. 7, fig. 2; Pl. 14, fig. 11). The expansion rate increases markedly, the umbilicus becomes proportionately smaller (34% of diameter). The umbilicus is relatively deep, with a subvertical wall and abruptly rounded shoulder. The sides are flattened and convergent, the venter arched. Ornament consists of fine, dense lirae which arise at the umbilical seam, pass forwards across the umbilical wall, shoulder and lower flank where they may branch, or where intercalated ribs may be inserted. The lirae flex gently backwards at mid-flank and forwards over the ventrolateral shoulders to form a broad shallow peak over the siphonal area. Shallow constrictions are present (? four per whorl), and each has a collar-like thickened rib parallel to it, and bearing lirae. The mould is smooth, save for constrictions. The suture line (Fig. 1) with large, incised, bifid lobes and saddles is of typical gaudryceratid type.

What may be an adult of this species is represented by a partially crushed specimen SAS FB11, 140 mm in diameter (Pl. 4). This shows a relative increase in whorl height and decrease in relative umbilical diameter. Ornament consists of strong wiry lirae which branch into twos and threes near the umbilical shoulder, and become very flexuous across the flanks.

DISCUSSION. The fragmentary specimen SAS Z999 demonstrates very clearly that *Gaudryceras cinctum* is no more than the adult of *Gaudryceras varicostatum*, as Spath suspected in 1922. The distinctive features of *G. varicostatum* are thus the *Vertebrites*-like inner whorls together with

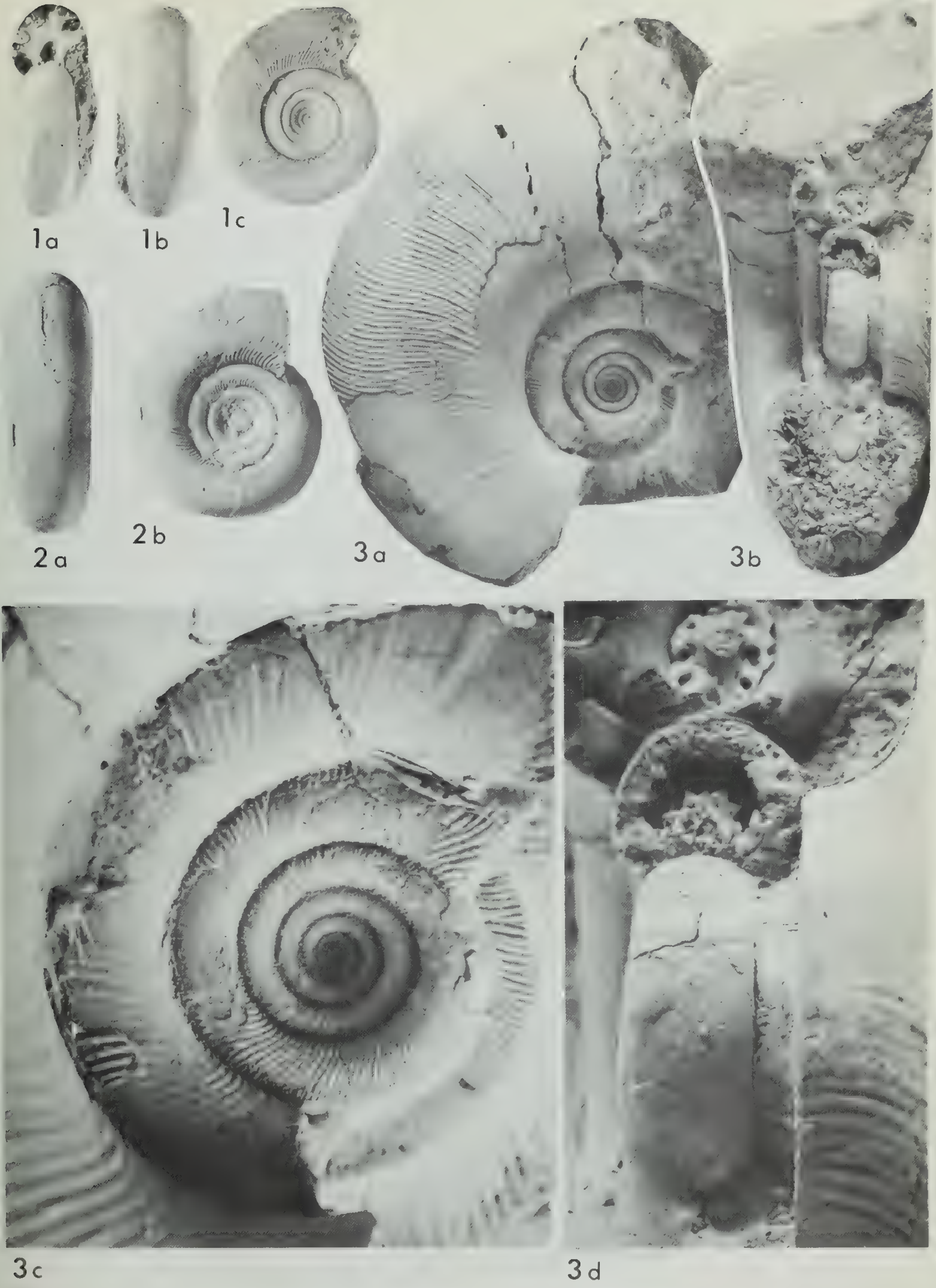

Plate 3 ×1, except Figs 3c–d

Figs 1–3 *Gaudryceras varicostatum* van Hoepen. Fig. 1, SAS P1418; Fig. 2, the **holotype**, TM 538; both late Santonian to early Campanian Umzamba Formation, Loc. 1, mouth of Umzamba River, southern Natal (Pondoland). Fig. 3, SAS Z999, St Lucia Formation, Coniacian II, Loc. 93, on farm Ncedomhlope, ESE of Hluhluwe, Zululand; Figs 3c–d ×3 to show details of juvenile ornament. See also Pl. 4; Pl. 7, fig. 2; Pl. 14, fig. 11.

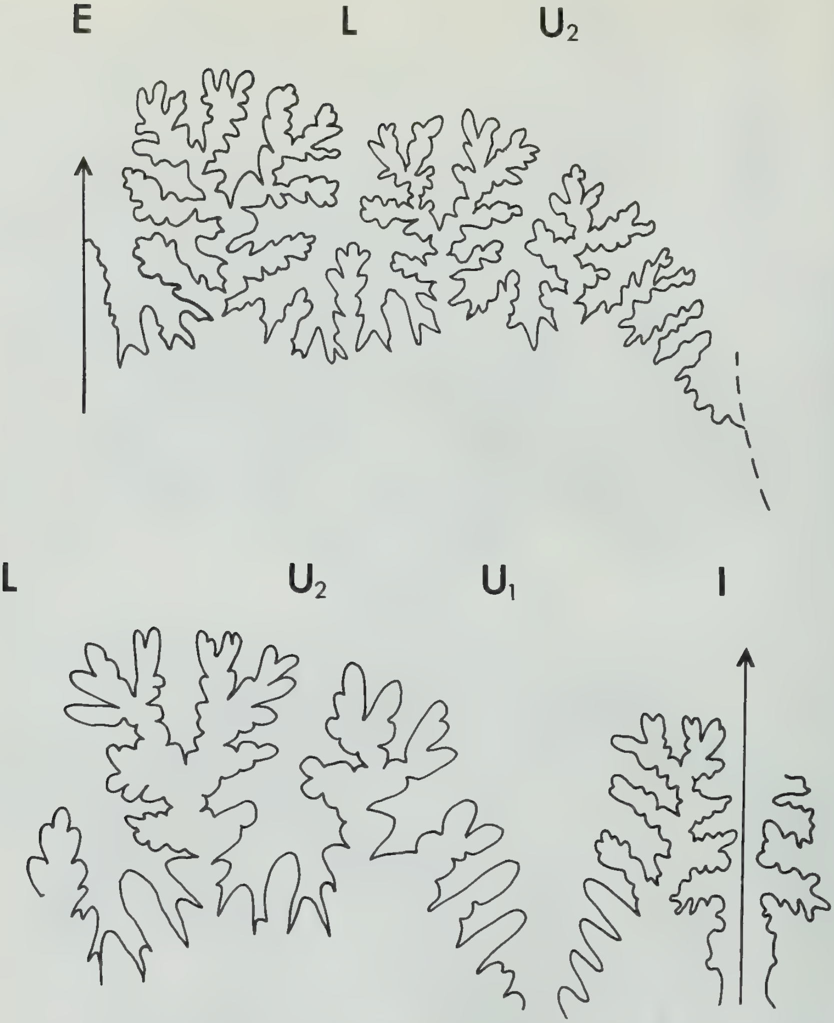

Fig. 1 Sutures of *Gaudryceras varicostatum* van Hoepen. TM 538, × 7½ approx.

typical *Gaudryceras*-like subsequent ornament, which place it clearly within the group of *G. mite*. There are obvious comparisons with *Gaudryceras stefaninii*, from which this species may well be descended, but there are more constrictions and a completely different whorl section in that species. Similar features separate *G. varicostatum* from *Gaudryceras varagurense*, as does the presence of more constrictions (six to eight per whorl), more evolute coiling and finer lirae in the latter. Differing relative proportions and coarseness of ornament also allow separation of medium-sized specimens from the superficially similar *Gaudryceras beantalyense* and *G. analabense*. *Gaudryceras striatum* Jimbo (1894 : pl. 6, fig. 6) and var. *pictum* Yabe (1903 : 33; pl. 4, fig. 6) are very finely ribbed and have many more collars and constrictions per whorl.

The poorly-known *Gaudryceras propemite* is said to have depressed whorls up to diameters of

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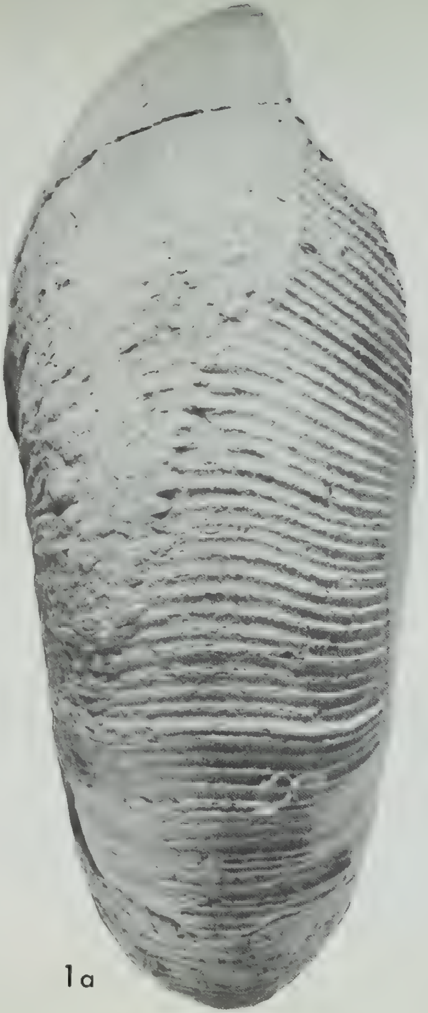
Plate 4 ×1

Gaudryceras varicostatum van Hoepen. SAS FB11, St Lucia Formation, southern part of False Bay, Zululand (precise horizon unknown, probably Coniacian or Santonian). See also Pl. 3; Pl. 7, fig. 2; Pl. 14, fig. 11.



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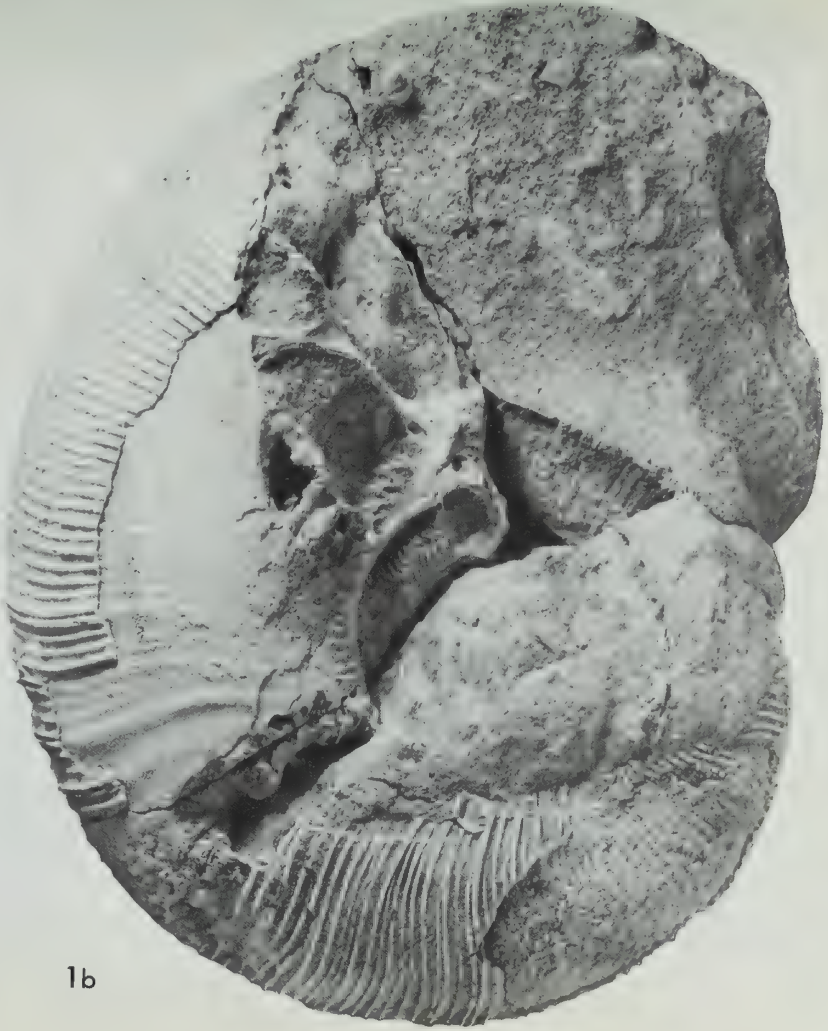


1b

60 mm; it is, however, probably a synonym of *G. cinctum*. *Gaudryceras anomalum* Collignon (1966 : 21; pl. 436, fig. 1891) is too poorly illustrated for comparison.

OCCURRENCE. Coniacian of Zululand, and late Santonian or early Campanian of Pondoland, Santonian of Madagascar and (?) Campanian of New Zealand.

Gaudryceras tenuiliratum Yabe

1890 *Lytoceras sacya* Forbes; Yokoyama : 178; pl. 18, figs 12, 13.
1903 *Gaudryceras tenuiliratum* Yabe : 19; pl. 3, figs 3–4; *non* var. *intermedia*: 27; pl. 3, fig. 1 (= *Gaudryceras denseplicatum*); ? var. *ornata*: 24; pl. 3, figs 2; ? var. *infrequens*: 28; pl. 4, figs 3a–3b.
1942 *Gaudryceras tenuiliratum* Yabe; Matsumoto : 667, fig. 1.
1942 *Gaudryceras tenuiliratum* Yabe var. *substriata* Matsumoto : 666 (nom nud).
1956 *Neogaudryceras tenuiliratum* (Yabe) Collignon : 69.
1963 *Gaudryceras tenuiliratum* Yabe; Jones : 26; pl. 9; pl. 10, figs 1–3; text-fig. 12.
? 1966 *Neogaudryceras* aff. *tenuiliratum* (Yabe); Collignon : 21; pl. 463, fig. 1891.

LECTOTYPE. Designated by Jones (1963 : 28), the original of *Lytoceras sacya* Yokoyama 1890 : 178, pl. 18, fig. 12.

MATERIAL. A single specimen, SAS Z1906, from the north-western part of the Nibela Peninsula, Lake St Lucia, Zululand, at 27° 57′ 00″ S, 32° 25′ 00″ E, and of Santonian age.

DESCRIPTION. The coiling is moderately evolute, less than 40% of the previous whorl being covered. The whorl section is rounded, slightly depressed during the early growth stages, becoming somewhat compressed as growth proceeds. Whorls expand slowly during early growth and rapidly during middle to late growth stages. The umbilicus is of medium size (approximately 40% of diameter) with a subvertical, outward-sloping umbilical wall merging into an evenly rounded shoulder.

The ornament of the early whorls is not well exposed in our specimen, but appears to consist of rather coarse, flexuous prorsiradiate lirae. There are periodic narrow flexuous prorsiradiate constrictions behind each of which is a strong collar-like rib. Lirae arise at the umbilical seam, sweep forwards across umbilical wall, shoulder and lower flank, backwards at mid-flank, and then forwards across the ventrolateral shoulders to form a broad, shallow peak on the venter. There are occasional constrictions, each preceded by a strong simple rib.

Partially exfoliated areas of the specimen show that ornament was very subdued on the internal mould. The suture line is not exposed, but there is a massive septal lobe.

DISCUSSION. The finely lirate inner and coarsely lirate outer whorls separate *G. tenuiliratum* from members of the *varagurense* and *denseplicatum* groups. The closest species is thus *Gaudryceras denmanense*, known from the Campanian of Vancouver Island, Alaska and Madagascar. Juveniles of the two species are said to be indistinguishable (Jones 1963 : 28) and the only obvious difference between adults is the development of coarse, simple ribs on the body chamber of *denmanense* which are never as flexuous as those of *tenuiliratum* and do not branch. These are trivial differences, whilst the species have overlapping geographic and stratigraphic ranges; large collections may show that they are no more than variants of a single species.

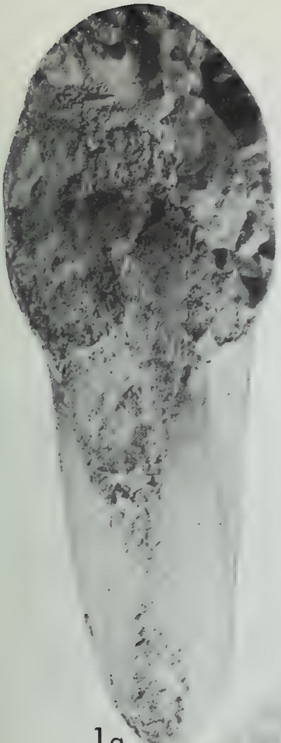
The position of *Gaudryceras tenuiliratum* vars *infrequens* and *ornata* is uncertain, as they are based on juveniles.

OCCURRENCE. Coniacian to Campanian of Japan, Santonian of Madagascar, Campanian of Alaska and Sakhalin, Santonian of South Africa (Zululand).

Plate 5 ×1

Figs 1–2 *Gaudryceras denseplicatum* (Jimbo). Fig. 1, TM 551, holotype of *Gaudryceras amapondense* van Hoepen, Umzamba Formation, late Santonian to early Campanian, Loc. 1, mouth of Umzamba River, southern Natal (Pondoland). Fig. 2, SAS H31, St Lucia Formation, Loc. 101, Hluhluwe River, Zululand (Santonian I–III). See also Pl. 6, fig. 2; Pl. 7, fig. 1.

Fig. 3 *Anagaudryceras politissimum* (Kossmat). SAS H202/1, St Lucia Formation, Loc. 87, False Bay, Lake St Lucia, Zululand (Santonian I–II).



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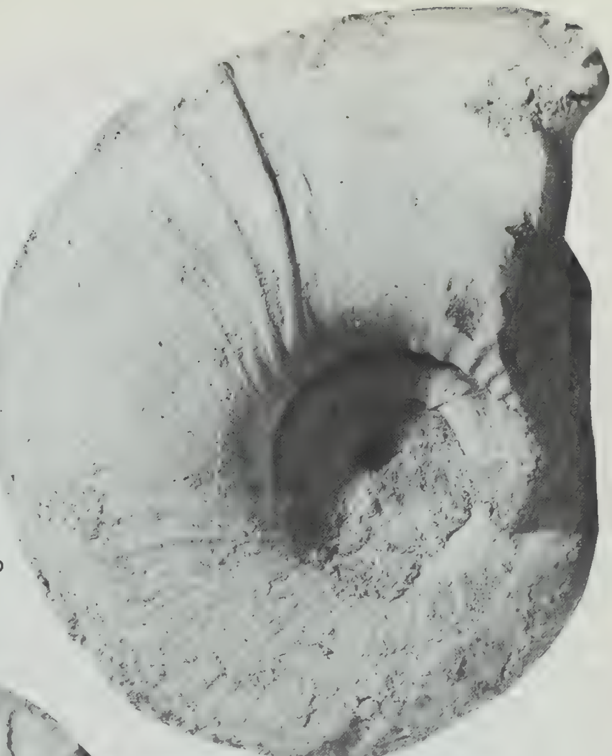

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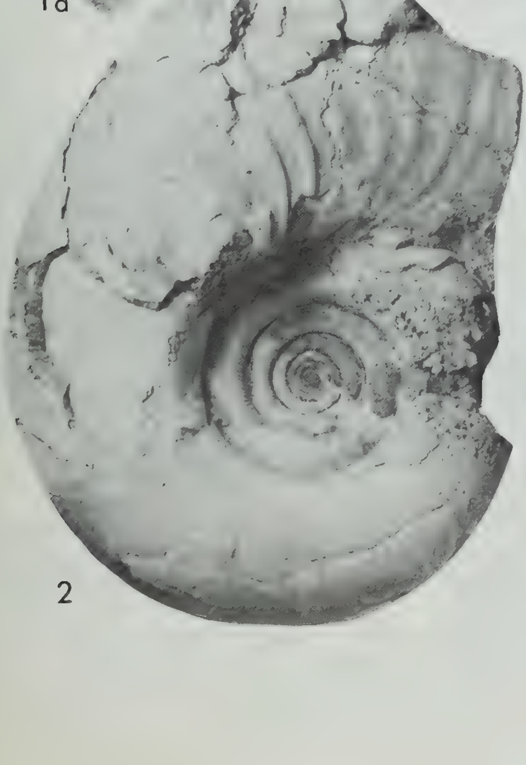

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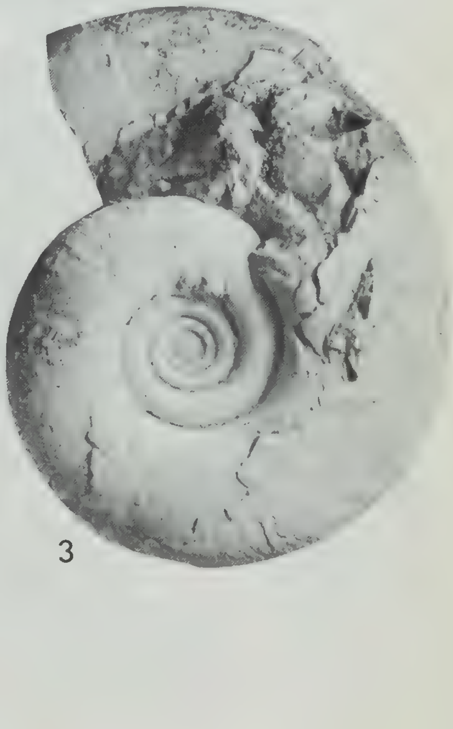

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Gaudryceras denseplicatum (Jimbo)
(Pl. 5, figs 1–2; Pl. 6, fig. 2; Pl. 7, fig. 1)

1894 *Lytoceras denseplicatum* Jimbo: 182; pl. 23, fig. 1.
1903 *Gaudryceras denseplicatum* (Jimbo) Yabe: 16, 30.
1903 *Gaudryceras tenuiliratum* var. *intermedia* Yabe: 27; pl. 3, figs 1a–1b.
1915 *Gaudryceras denseplicatum* (Jimbo); Yabe: 13.
1920 *Lytoceras* (*Gaudryceras*) *amapondense* van Hoepen: 42; pl. 24, figs 1–3.
1921*b* *Gaudryceras amapondense* van Hoepen; Spath: 50 (table).
1922 *Gaudryceras amapondense* van Hoepen; Spath: 118.
? 1924 *Neogaudryceras denseplicatum* (Jimbo) *nonstriata* Yehara: 35; pl. 2, fig. 1.
? 1942 *Neogaudryceras denseplicatum* (Jimbo) var. *kawadai* Matsumoto: 666 (nom. nud).
1956 *Neogaudryceras denseplicatum* (Jimbo); Collignon: 60; pl. 9, fig. 1.
1959 *Gaudryceras glaneggense* (Redtenbacher); Wiedmann: 715.
1962*a* *Gaudryceras vascogoticum* Wiedmann: 159; pl. 9, figs 2, 6; text-fig. 17.
1965*b* *Neogaudryceras denseplicatum* (Jimbo); Collignon: 6; pl. 416, fig. 1719.

MATERIAL. Seven specimens. TM 551 (the holotype of *Gaudryceras amapondense* van Hoepen), TM 558, SAS P7/1 and SAM 7094, from the late Santonian to early Campanian Umzamba Formation at Loc. 1, the mouth of the Umzamba River, southern Natal (Pondoland); SAS H-30-3 from Loc. 100 and SAS H31 from Loc. 101 on the Hluhluwe River, Zululand (Santonian I–III); SAS Z1154 from Loc. 114 on the Nibela Peninsula, Zululand (Campanian II) and Z337 from the west bank of the Hluhluwe River at 28° 05′ 00″ S, 32° 15′ 00″ E (Upper Coniacian ?). All the Zululand material is from the St Lucia Formation.

DESCRIPTION. *Early growth stages, up to 60 mm* (Pl. 5, fig. 2). The coiling is evolute, the whorl section as high as broad, or slightly compressed, the greatest breadth being just above the umbilical shoulder. The flanks are gently rounded, converging to an arched, evenly rounded venter. The umbilicus is broad (about 50% of diameter) and of moderate depth, with a high wall and abruptly rounded shoulder. The test is ornamented by fine, dense, prorsiradiate flexuous lirae, clearly visible to the naked eye, and arising at the umbilical seam. They flex forwards over the lower part of the flank and backwards at mid-flank to sweep forwards across the ventrolateral shoulders to form a distinct peak over the siphonal region. There are periodic strengthened ribs, corresponding to shallow prorsiradiate constrictions on the internal mould, which is otherwise smooth.

Later growth stages (Pl. 5, fig. 1; Pl. 6, fig. 2). At diameters greater than 60 mm, the type of ornament described above gives way to narrow, rounded, flexuous ribs which increase in strength as diameter increases. These are rather irregularly spaced, with interspaces typically much wider than the ribs themselves. The ribs arise at the umbilical seam, strengthen across the umbilical wall, are prorsiradiate on the lower flank, first sweep gently forwards, then flex backwards across the upper flank and forwards across the ventrolateral shoulder to form a strong ventral peak, where they are thickened into a lip-like process. Both ribs and interspaces are covered in fine, dense lirae, like those of the early growth stages, when shell is preserved. Exfoliated specimens or internal moulds show only the strong ribs (Pl. 5, fig. 2).

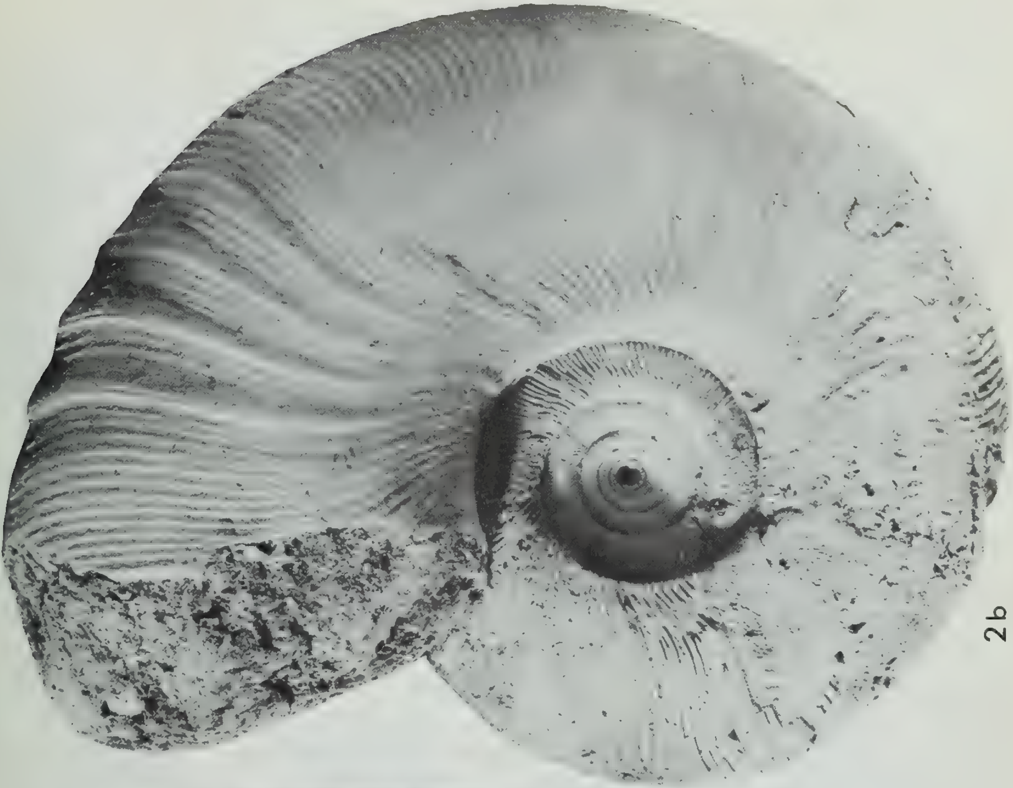
The suture line consists of deeply incised bifid lobes and saddles, and a retracted suspensive lobe with several auxiliary elements.

Plate 6 × 1, except Fig. 1

Fig. 1 '*Gaudryceras*' *sigcau* van Hoepen. Lateral view of **holotype,** TM 560, late Santonian to early Campanian Umzamba Formation, Loc. 1, mouth of Umzamba River, southern Natal (Pondoland), × 2·5.

Fig. 2 *Gaudryceras denseplicatum* (Jimbo). SAS P7/1, Umzamba Formation (Santonian III ?), Loc. 1, mouth of Umzamba River, southern Natal (Pondoland). See also Pl. 5, figs 1–2; Pl. 7, fig. 1.

Figs 3–4 *Anagaudryceras pulchrum* (Crick). Fig. 3, SAS U1; Fig. 4, SAS 57; both Mzinene Formation (Albian V ?), Mzinene River, Zululand. See also Pl. 12, figs 1–3, 5–10; Pl. 13.



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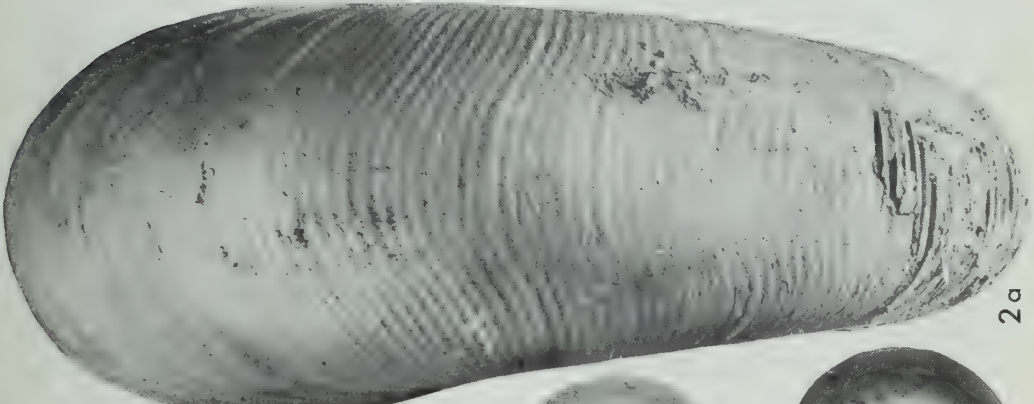

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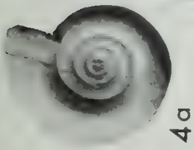

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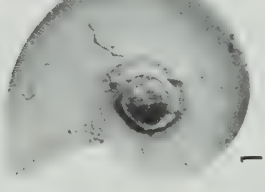

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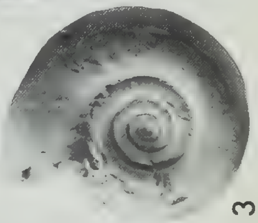


3

DISCUSSION. The striking change from juvenile to adult ornament clearly separates *Gaudryceras densеplicatum* from members of the *mite* and *tenuiliratum* groups. Comparisons with other members of the *denseplicatum* group are as follows.

Gaudryceras glaneggense (Redtenbacher 1873: 119; pl. 28, figs 3a–b; see also Collignon 1956: 62; 1965*b*: 4; pl. 414, fig. 1716) is a rather poorly known European species, since re-illustrated on the basis of specimens from Madagascar. It is separated from the present species on the basis of stronger, more widely spaced, more flexuous ribs, with far more intermediate lirae.

Gaudryceras lauteli (Collignon) by contrast develops only occasional fold-like ribs, and these only on the last part of the body chamber. *Gaudryceras tenuiliratum* var. *intermedia*, *Gaudryceras vascogoticum* Wiedmann and the crushed and poorly-preserved *Gaudryceras amapondense* (van Hoepen) are clear synonyms of *G. denseplicatum*.

OCCURRENCE. Coniacian to Campanian of Zululand and Pondoland, Coniacian of Madagascar, Turonian to Coniacian of Japan, Coniacian of northern Spain.

'Gaudryceras' sigcau van Hoepen
(Pl. 6, fig. 1)

1921 *Gaudryceras sigcau* van Hoepen: 9; pl. 2, figs 13–16; text-fig. 5.
1922 *Gaudryceras sigcau* van Hoepen; Spath: 118.
1956 *Gaudryceras sigcau* van Hoepen; Collignon: 170.

HOLOTYPE. TM 560, figured by van Hoepen (1921) as pl. 2, figs 13–16.

MATERIAL. The holotype TM 560 and paratype TM 561, both from the Umzamba Formation of late Santonian to early Campanian age, at Loc. 1, the mouth of the Umzamba River, southern Natal (Pondoland).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wh/Wb*	*U*
TM 560	11·6	4·5 (39)	4·6 (40)	0·99	3·9 (39)
TM 561	11·1	4 (36)	4·7 (42)	0·85	4 (36)

DISCUSSION. Van Hoepen (1921: 9) provides a detailed description of this species, which is based upon juveniles just over a centimetre in diameter. As a result of their small size, it is difficult to place the specimens with certainty in any gaudryceratid genus, or to discuss their actual position. A specimen is refigured as Pl. 6, fig. 1.

'Gaudryceras' spp.
(Pl. 12, figs 4, 11)

1907*b* *Gaudryceras* sp. Crick: 238; pl. 15, figs 4, 4a.
1907*b* *Gaudryceras* sp. Crick: 239.

MATERIAL. Two specimens, BM(NH) C18271 and C18269, from the Munywana Creek, Zululand.

DISCUSSION. These two indeterminate fragments cited by Crick are here figured as Pl. 12, figs 4, 11 respectively. They are generically indeterminate. Both specimens are probably of Albian age.

Genus *ANAGAUDRYCERAS* Shimizu, 1934

TYPE SPECIES. *Ammonites sacya* Forbes 1846, by the original designation of Shimizu (1934: 67); subjective synonym of *Ammonites buddha* Forbes (1846: 112; pl. 14, fig. 9).

SYNONYMY. *Paragaudryceras* Shimizu, 1934 (type species *Paragaudryceras limatum* Yabe 1903, by original designation); *Murphyella* Matsumoto, *in* Matsumoto, Muramoto & Takahashi 1972 (type species *Kossmatella* (*Murphyella*) *enigma* Matsumoto, Muramoto & Takahashi 1972, by original designation).

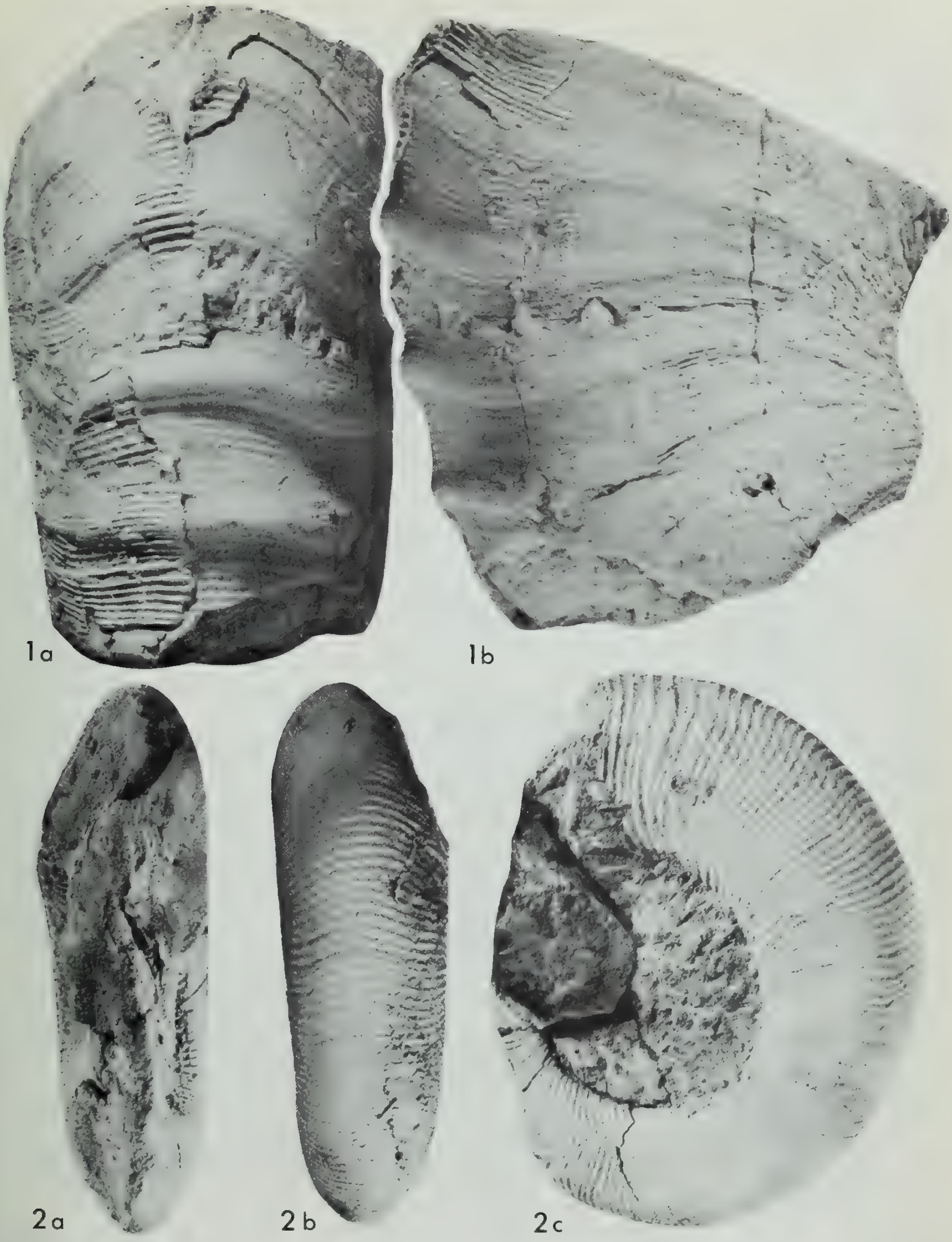


Plate 7 ×1

Fig. 1 *Gaudryceras denseplicatum* (Jimbo). SAS 337, St Lucia Formation (Upper Coniacian ?), west bank of Hluhluwe River at 28° 05′ 00″ S, 32° 15′ 00″ E. See also Pl. 5, figs 1–2, Pl. 6, fig. 2.

Fig. 2 *Gaudryceras varicostatum* van Hoepen. SAS Z1157, St Lucia Formation, close to Loc. 114, SW tip of Nibela Peninsula, Zululand (Campanian II). See also Pls 3, 4; Pl. 14, fig. 11.

DIAGNOSIS. Medium-sized gaudryceratids in which the early growth stages show an evenly rounded, circular to depressed whorl section which may become compressed in later growth stages. Ornament of early and middle growth stages typically consists of very fine radial lirae, often invisible to the naked eye, and periodic rounded, collar-like radial ribs. Internal moulds are typically smooth, save for radial constrictions corresponding to the site of the periodic ribs. Ornament frequently changes on the body chamber, where constrictions become closely spaced and fold- or scale-like ribs develop between them. Suture line gaudryceratid, with deeply incised, bifid lobes and saddles and a retracted suspensive lobe.

DISCUSSION. Nomenclatoral problems associated with the erection of *Anagaudryceras* have been reviewed by Wright & Matsumoto (1954 : 111–113) and the interpretation of the genus is discussed by Matsumoto (1959*a* : 138; 1959*b* : 73), Wiedmann (1962*a* : 156–158) and Howarth (1965 : 357). The difficulty stems mainly from the fact that the type specimen of *Anagaudryceras sacya* (Pl. 8, fig. 3) is a poorly-preserved juvenile which could conceivably be referred to a number of other genera. If current interpretations of *Ammonites buddha* Forbes as the adult of this species are valid, then *Anagaudryceras* is in our view sufficiently different from other gaudryceratids to be given generic status. If, however, this is found not to be the case when topotype material is redescribed, then most of the forms described here will be referable to *Paragaudryceras* Shimizu, 1934.

Of the most similar genera, *Gaudryceras* de Grossouvre, 1894, is characterized by fine but distinct sigmoid lirae or riblets which are strongly projected on the venter. *Mesogaudryceras* Spath, 1927, is very compressed, with flexuous lirae and no constrictions. *Zelandites* Marshall, 1926, is compressed with many constrictions and virtually no ornament at any stage.

Kossmatella Jacob, 1907, can normally be distinguished by its smaller size and the presence of constrictions and lateral fold-like ribs throughout ontogeny. There are, however, some species with morphologically intermediate characters, which require comment. Thus '*Kossmatella*' *whitneyi* Gabb (1869 : 134; pl. 22, figs 14–14b) may be an *Anagaudryceras* (Murphy 1967*b* : 16), whilst *Kossmatella gainesi* Anderson (1938 : 153; pl. 20, figs 3–5), referred to *Eotetragonites* by Murphy (1967*b* : 23), also shows features recalling *Anagaudryceras buddha*.

Jauberticeras Jacob, 1907, has a depressed whorl section with a sharp lateral angle at some stage, very evolute coiling, slowly expanding whorls, and is typically ornamented by lirae. It is readily distinguished from *Anagaudryceras* (Murphy 1967*c*).

Matsumoto (*in* Matsumoto, Muramoto & Takahashi 1972) has recently introduced the subgenus *Kossmatella* (*Murphyella*), type species *K.* (*M.*) *enigma* Matsumoto, Muramoto & Takahashi (1972 : 210; pl. 33, figs 1–3; text-fig. 1), for gaudryceratids characterized by *Kossmatella*-like ribs on their inner whorls, relatively smooth middle growth stages, and fold-like ribs on the adult whorl. It is quite clear from the material referred below to *Anagaudryceras buddha* (Forbes) that these same ontogenetic changes are seen in typical *Anagaudryceras*, and we would regard *Murphyella* as a synonym of *Anagaudryceras*.

The currently-held view on the origin of *Anagaudryceras* is that it evolved from *Eogaudryceras* (*Eogaudryceras*) during the early Albian; it is therefore of some interest that our collections contain large numbers of specimens of low Middle Albian age, amongst the earliest records of the genus. *Eogaudryceras* (*Eogaudryceras*) differs from *Anagaudryceras* in having constrictions only on the inner whorls, and lacking fold-like ribs when adult. *Eogaudryceras* (*Eotetragonites*) bears frequent oblique constrictions throughout ontogeny.

About twenty-five species of *Anagaudryceras* or '*Paragaudryceras*' have been proposed; the majority are listed by Collignon (1956 : 68–70), to which can be added *Anagaudryceras particostatum* Marshall (1926 : 143; pl. 20, fig. 7; pl. 30, figs 3–4), *Anagaudryceras tennanti* Henderson (1970 : 10; pl. 2, figs 4, 7), *Anagaudryceras coagmentum* Collignon (1963 : 20; pl. 249, fig. 1064), *Anagaudryceras pulvinatum* Collignon (1964: 12; pl. 324, fig. 1445) and *Anagaudryceras yokoyamaiforme* Collignon (1966 : 12; pl. 516, fig. 2031).

Many of these are based upon juveniles at the *sacya* stage, and their reference to *Anagaudryceras* rather than *Gaudryceras* is questionable; others are based upon only a few specimens, so that intraspecific variability is poorly understood. Howarth (1965 : 358) provides an excellent

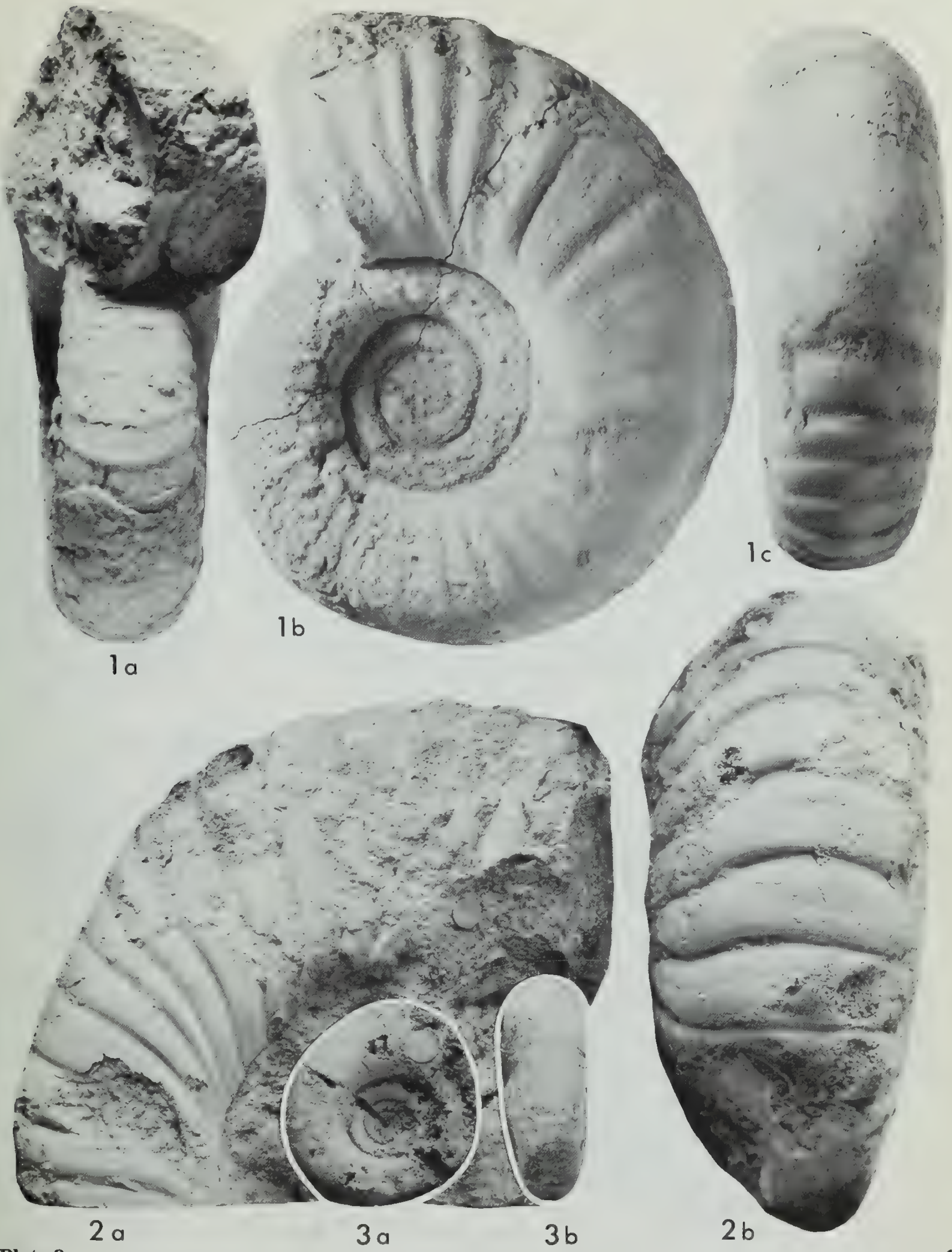


Plate 8 ×1

Figs 1, 2, 3 *Anagaudryceras buddha* (Forbes). Fig. 1, SAS A1402, Mzinene Formation, Albian III, Loc. 36, Mzinene River, Zululand. Fig. 2, the **holotype,** BM(NH) C22673, Utatur Group of Verdachellum, southern India, figd Forbes (1846 : pl. 14, fig. 9). Fig. 3, holotype of *A. sacya* (Forbes), BM(NH) C51067, from the same formation, also figd Forbes (1846 : pl. 14, fig. 10). See also Pls 9, 10; Pl. 11, figs 1–2.

discussion of the principal 'species' groups, which may correspond to no more than long-ranging species. These may be summarized as follows.

1. The group of *Anagaudryceras buddha*, with strong, fold-like ribs on the body chamber, including: *A. buddha* (Forbes 1846 : 112; pl. 14, fig. 9) [= *A. sacya* (Forbes 1846 : 113; pl. 14, fig. 10)], Albian to Coniacian. *A. subsacya* Marshall (1926 : 144; pl. 20, figs 8–8a; pl. 29, figs 1–2), Campanian. *A. mokharaense* (Collignon 1950 : 67; pl. 11, figs 1–2; pl. 12, fig. 5), Upper Albian. *A. sakalavum* (Collignon 1949 : 51; pl. 7, figs 3–3b), Albian. *A. aurarium* (Anderson 1938 : 151; pl. 20, figs 1, 2), Albian. *A. coagmentum* (Collignon 1963 : 20; pl. 249, figs 1064), Albian. *A. luneburgense* (Schlüter 1872 : 62; pl. 18, figs 8–9), Campanian. *A. limatum* (Yabe 1903 : 34; pl. 14, fig. 2; pl. 5, fig. 2; pl. 6, figs 3a–b). *A. revelatum* (Stoliczka 1865 : 152; pl. 75, figs 3–3b), Albian–Cenomanian. *A. salinarium* (Douvillé 1931 : 42; pl. 1, fig. 3; text-fig. 5), Cenomanian.

2. The group of *Anagaudryceras involvulum*, typically compressed during later growth and retaining weak ornament apparently throughout ontogeny, including: *A. involvulum* (Stoliczka 1865 : 150; pl. 75, figs 1–1b), Cenomanian–Turonian. *A. madraspatanum* (Stoliczka 1865 : 151; pl. 75, figs 2–2c), Albian–Cenomanian. *A. utaturense* (Shimizu 1935) [= *Ammonites sacya* Forbes; Stoliczka 1865, pars], Cenomanian. *A. pulchrum* (Crick 1907b : 237; pl. 15, figs 1–1a), Albian. *A. politissimum* (Kossmat 1895 : 128; pl. 15, figs 7–7c), Turonian–Santonian. *A. yamashitai* (Yabe 1903 : 38; pl. 4, fig. 7), Santonian. *A. mikobokoense* (Collignon 1956 : 59; pl. 8, figs 1–1b), Campanian. *A. particostatum* (Marshall 1926 : 143; pl. 20, fig. 7; pl. 30, figs 3, 4), Campanian. *A. tennanti* Henderson (1970 : 19; pl. 2, figs 4–7; text-fig. 5b), Campanian. *A. subtilineatum* (Kossmat 1895 : 123; pl. 19, figs 1a–c, 2a–b), Santonian–Campanian. *A. multiplexum* (Stoliczka 1865 : 154; pl. 76, fig. 1–1b), Cenomanian.

OCCURRENCE. The known time range of *Anagaudryceras* is from Middle Albian to Maastrichtian. The geographical distribution includes Antarctica, New Zeland, Zululand, Madagascar, Angola, north Africa, France, Germany, Austria, Romania, southern India, Japan, Sakhalin, Kamchatka, Alaska, British Columbia and California.

Anagaudryceras buddha (Forbes)

(Fig. 2; Pl. 8, figs 1–3; Pl. 9, figs 1–3; Pl. 10, figs 1–6, Pl. 11, figs 1–2)

1846 *Ammonites buddha* Forbes : 112; pl. 14, fig. 9.
1846 *Ammonites sacya* Forbes : 113; pl. 14, fig. 10.
1865 *Ammonites sacya* Forbes; Stoliczka : 154; pl. 75, figs 5–7 (*non* pl. 76, figs 2–3, = *Gaudryceras multiplexum* (Kossmat).
1865 *Ammonites revelatus* Stoliczka : 152; pl. 75, fig. 3.
1869 *Ammonites whitneyi* Gabb : 134; pl. 22, figs 14–14b.
1876 *Ammonites filicinctus* Whiteaves : 43; pl. 2, figs 2a–c, 3.
1879 *Ammonites filicinctus* Whiteaves; Whiteaves : 104 (footnote).
1884 *Lytoceras sacya* (Forbes) Whiteaves : 203; pl. 25.
non 1890 *Lytoceras sacya* (Forbes); Yokoyama : 178; pl. 8, figs 12, 13 (= *Gaudryceras tenuiliratum* Yabe).
non 1894 *Lytoceras sacya* (Forbes); Jimbo : 34; pl. 6, fig. 1 (= *Gaudryceras tenuiliratum* Yabe).
1895 *Lytoceras* (*Gaudryceras*) *sacya* (Forbes); Kossmat : 119.
1895 *Lytoceras* (*Gaudryceras*) *revelatum* (Stoliczka) Kossmat : 128.
? 1897 *Ammonites sacya* Forbes; Simionescu : 271.
? 1902 *Lytoceras* (*Gaudryceras*) *sacya* (Forbes); Anderson : 82.
1903 *Gaudryceras sacya* (Forbes); Yabe : 17.
1903 *Gaudryceras limatum* Yabe : 34; pl. 4, fig. 2; pl. 5, fig. 2; pl. 6, fig. 3.
1903 *Lytoceras* (*Gaudryceras*) *sacya* (Forbes); Choffat : 14; pl. 1, figs 2, 3.
? 1906 *Gaudryceras* cf. *sacya* (Forbes); Boule, Lemoine & Thévenin : 184; pl. 2, fig. 2.
? non 1907*a* *Gaudryceras* aff. *sacya* (Forbes); Crick : 170; pl. 10, fig. 13.
? 1913 *Gaudryceras* cf. *sacya* (Forbes); Petković : 51; pl. 1, figs 1–2.
? 1917 *Gaudryceras sacya* (Forbes); Woods : 170; pl. 10, figs 13–13A) (= *Anagaudryceras* sp. nov. according to Henderson 1970 : 19).
1921*b* *Paragaudryceras buddha* (Forbes) Spath : 41.
1934 *Anagaudruceras sacya* (Forbes) Shimizu : 67.

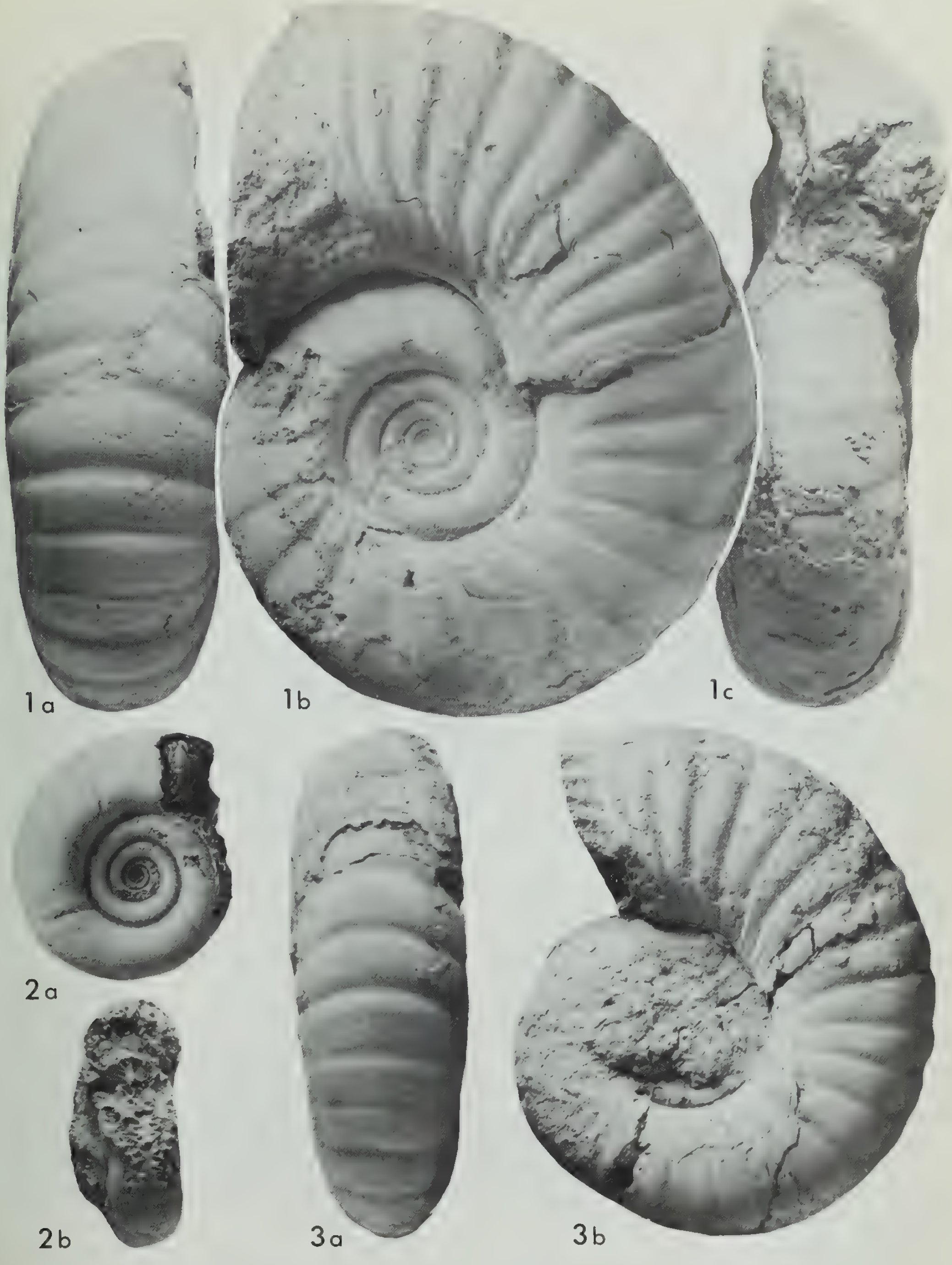


Plate 9 ×1

Figs 1–3 *Anagaudryceras buddha* (Forbes). Fig. 1, BM(NH) C78746; Fig. 2, BM(NH) C78742; Fig. 3, SAS A2118; all Mzinene Formation, Albian III, Loc. 35, Mzinene River, Zululand. See also Pls 8, 10; Pl. 11, figs 1–2.

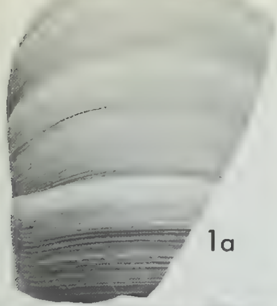
1935 *Gaudryceras choffati* Shimizu: 116.
1936 *Gaudryceras* (*Paragaudryceras*) *buddha* (Forbes); Breistroffer *in* Besairie: 167, fig. 10a.
non 1936 *Lytoceras* (*Gaudryceras*) *sacya* (Forbes); Venzo: 78; pl. 5, figs 5a–5b (= *Anagaudryceras pulchrum* Crick).
1938 *Lytoceras* (*Kossmatella*) *whitneyi* (Gabb) Anderson: 152; pl. 31, figs 1, 2.
1950 *Gaudryceras* (*Paragaudryceras*) *buddha* (Forbes); Collignon: 38; pl. 6, fig. 5.
? 1950 *Gaudryceras* (*Paragaudryceras*) *mokharaense* Collignon: 67; pl. 11, figs 1–2; pl. 12, fig. 5.
1953 *Paragaudryceras buddha* (Forbes); Spath: 10.
1953 *Anagaudryceras* sp. nov. Spath: 10–11.
1954 *Anagaudryceras sacya* (Forbes); Wright & Matsumoto: 112.
1957 *Anagaudryceras sacya* (Forbes); Wright: L200, fig. 230, 4.
1959*b* *Anagaudryceras sacya* (Forbes); Matsumoto: 72; pl. 22, figs 4, 5a–c.
1960 *Kossmatella cappsi* Imlay: 99; pl. 12, figs 17–22.
? 1963 *Paragaudryceras coagmentum* Collignon: 20; pl. 249, fig. 1064.
1964 *Gaudryceras sacya* auctt.; Collignon: 4; pl. 318, fig. 1351.
1965 *Paragaudryceras buddha* (Forbes); Thomel: 138, table 2.
1965 *Anagaudryceras sacya* (Forbes); Howarth: 358.
1967 *Anagaudryceras sacya* (Forbes); Jones: 23; pl. 1, figs 5–7, 13–15.
1967*b* *Anagaudryceras* sp. Murphy: 15; pl. 2, figs 1, 2, 4.
1967*b* *Anagaudryceras whitneyi* (Gabb) Murphy: 16; pl. 2, figs 3, 5, 6.
1972 *Anagaudryceras sacya* (Forbes); McLearn: 28; pl. 5, figs 3a–b, 4; pl. 6, fig. 4; pl. 16, figs 2, 3, 4; pl. 17, figs 1–2; pl. 43, figs 1a–c.
1972 *Anagaudryceras* cf. *sacya* (Forbes); McLearn: 33; pl. 6, figs 3a–b; pl. 40, figs 2a–c.
1972 *Anagaudryceras filicinctum* (Whiteaves) McLearn: 33, 34; pl. 17, fig. 3, 4a–c; pl. 19, figs 1–2; pl. 36, fig. 2.
1972 *Anagaudryceras* sp. McLearn: 35; pl. 19, figs 3a–b.
1972 *Kossmatella* (*Murphyella*) *enigma* Matsumoto, Muramoto & Takahashi: 210; pl. 33, figs 1–3; text-fig. 1.

Holotype. Forbes' original specimen, BM(NH) C22673, from Verdachellum in southern India, refigured here as Pl. 8, figs 2a–b.

Material. We have a large number of specimens: SAS A13, A1218, A1323–4, A1326–8, A1410, A1417, A1428, A1586, A1616 and BM(NH) C78719–C78747 from the Mzinene Formation at Loc. 35 and BM(NH) C78748–C78752 from Loc. 36 on the Mzinene River (Albian III); BM(NH) C78753–4 from Bed 11 or 12 of the Mzinene Formation, Loc. 51 on the Mzinene (Albian V) and SAS Z36 from the same locality (previous horizon unknown, Albian IV–V). BM(NH) C18140 referred to and figured by Crick (1907*a*) as *Gaudryceras* aff. *sacya* Forbes appears to belong to some other species (Pl. 1, fig. 9).

Dimensions.	*D*	*Wb*	*Wh*	*Wb*/*Wh*	*U*
BM(NH) C51067 (holotype of *A. sayca*)	32·0 ?	13·0 (41)	11·2 (35)	1·16	13·1 (41)
BM(NH) C78742	35·8	14·3 (39)	11·9 (33)	1·20	16·0 (44)
BM(NH) C78743	47·7	17·6 (37)	17·3 (36)	1·02	19·7 (41)
SAS A1404	47·8	19·3 (40)	16·2 (34)	1·19	20·0 (42)
BM(NH) C78744	50·0	18·7 (37·4)	17·8 (35·6)	1·05	20·3 (41)
BM(NH) C78745	51·0	20·0 (39)	19·4 (38)	1·03	19·7 (39)
SAS A1403	55·0	22·0 (40)	22·0 (40)	1·0	19·4 (35)
SAS A1402	79·0	31·0 (39)	31·5 (40)	0·98	29·4 (37)
SAS 1218	80·5	–	30·8 (38)	–	28·3 (35)
BM(NH) C78746	101·0	–	37·8 (37)	–	38·0 (38)
BM(NH) C78747	102·0	37·7 (37)	38·5 (38)	0·98	36·4 (36)

Description. *Early growth stages, up to 30–40 mm diameter.* The coiling is very evolute, with a slightly depressed whorl section (whorl breadth/height ratio up to 1·20), the greatest breadth being a little way below mid-flank. The umbilicus is broad (up to 44% of diameter) with a low, rounded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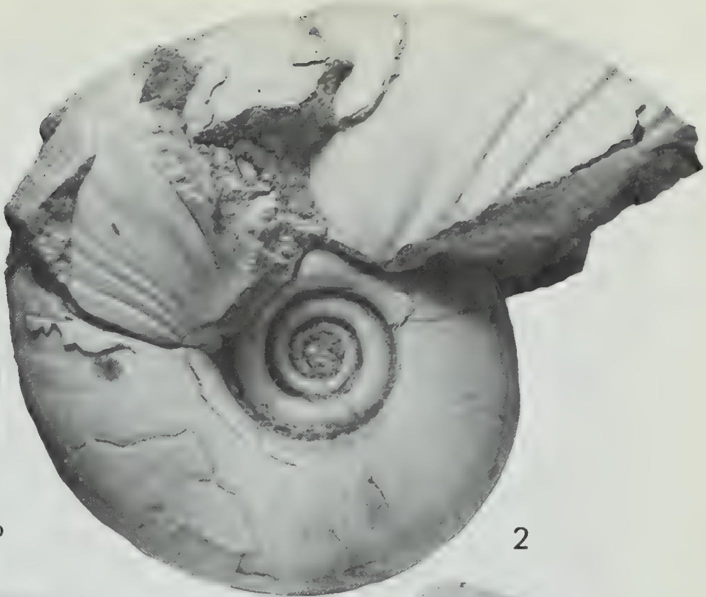
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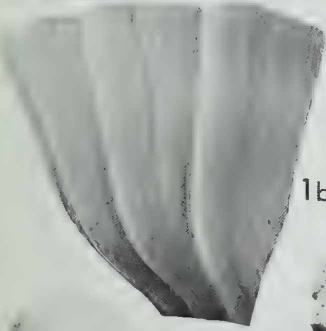
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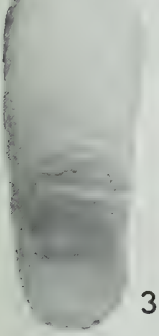
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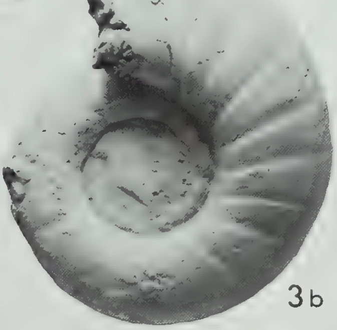
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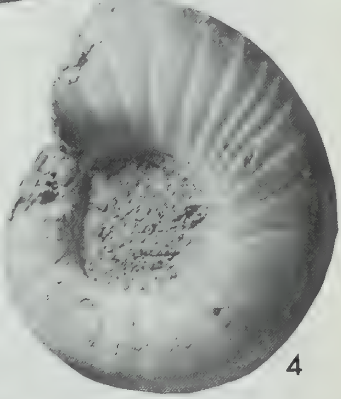
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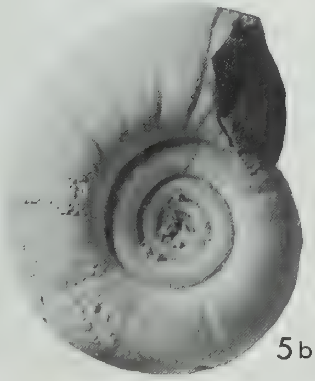
5a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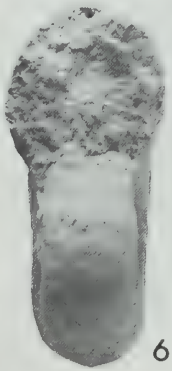
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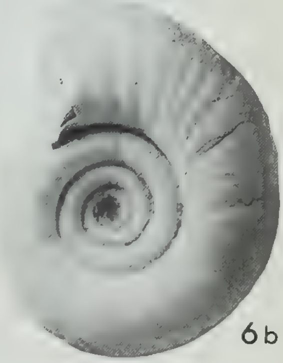

6b

Plate 10 × 1, except Fig. 1

Figs 1–6 *Anagaudryceras buddha* (Forbes). Fig. 1, BM(NH) C78753, Mzinene Formation, Albian V, Loc. 51, Bed 12 or 13, Mzinene River, Zululand: × 2 to show details of lirae on shell surface. Fig. 2, SAS Z36 from same locality; Albian IV–V, precise horizon unknown. Fig. 3, BM(NH) C78745; Fig. 4, SAS A1403; Fig. 5, BM(NH) C78744; Fig. 6, BM(NH) C78743; all Mzinene Formation, Albian III, Loc. 35, Mzinene River, Zululand. See also Pls 8, 9; Pl. 11, figs 1–2.

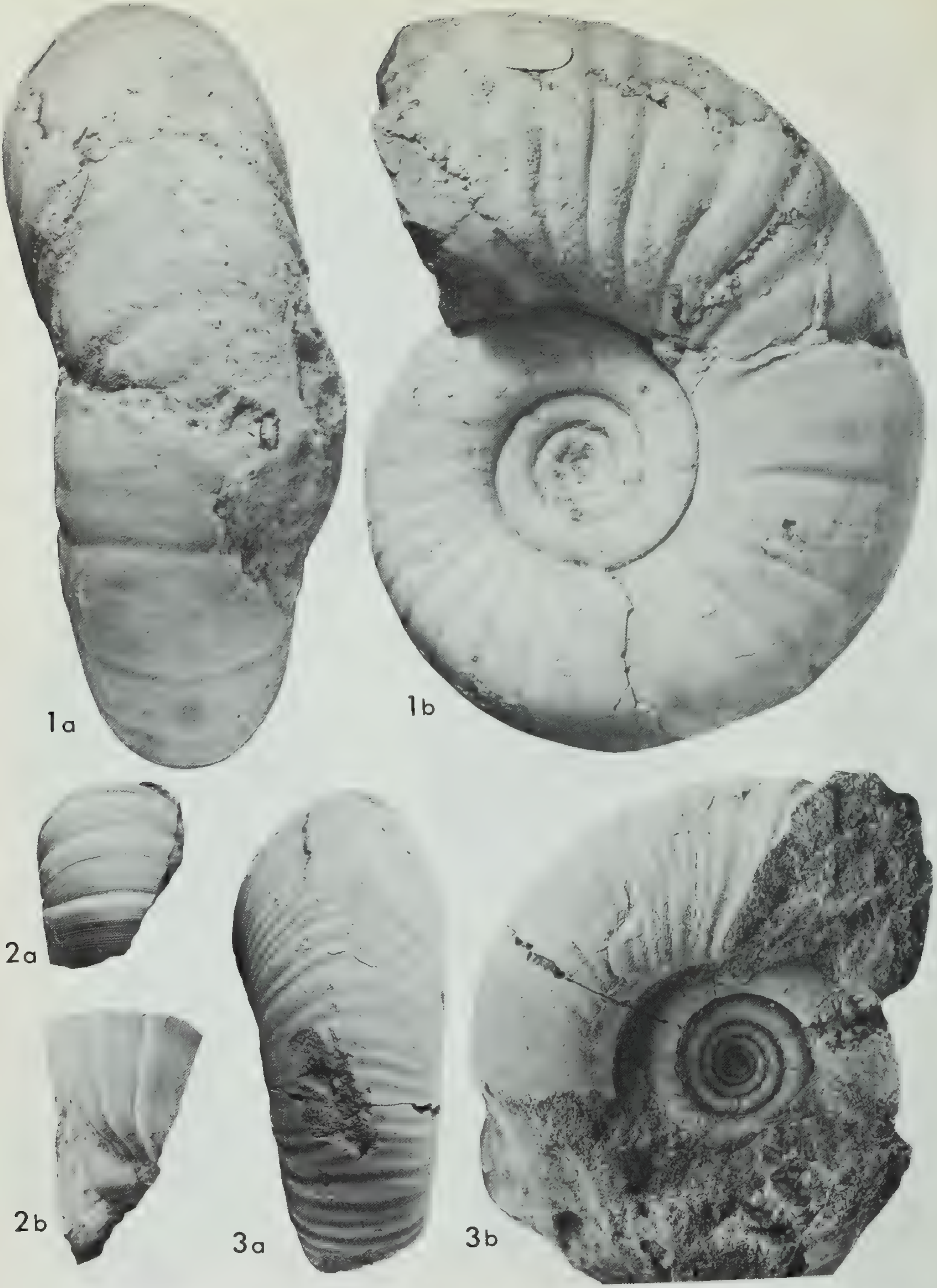


Plate 11 ×1

Figs 1–2. *Anagaudryceras buddha* (Forbes). Fig. 1, BM(NH) C78747, Mzinene Formation, Albian III, Loc. 35; Fig. 2, BM(NH) C78753, Mzinene Formation, Albian V, Loc. 51, Bed 12 or 13, Mzinene River, Zululand. See also Pls 8–10.

Fig. 3 *Anagaudryceras subsacya* (Marshall). UND 635, Umzamba Formation, Santonian or Campanian, Loc. 4, Sometsu Road, Durban.

umbilical wall, merging with rounded, convergent flanks. The ventrolateral shoulders are rather abruptly rounded, and the venter somewhat flattened.

The shell surface is ornamented by very fine lirae which arise at the umbilical seam, pass straight up the umbilical wall, are markedly prorsiradiate and weakly convex across the flank, flexing gently backwards across the ventrolateral shoulder to cross the venter with a shallow broad peak. There are up to six broad, low, rounded collar-like ribs per whorl, running parallel to the lirae, and in front of each is a shallow constriction. Both collar and constriction are covered in lirae.

Internal moulds are smooth, save for low swellings, corresponding to the site of collars, and shallow constrictions, rather more prominent than those on the shell surface.

Middle growth stages, 30–50 mm. As size increases, the whorl section tends to become as high as wide, and as a result the umbilicus becomes proportionately smaller. The test is ornamented by fine lirae and periodic collars and constrictions as in the early growth stages, but the latter become progressively more closely spaced and distinctly flexuous.

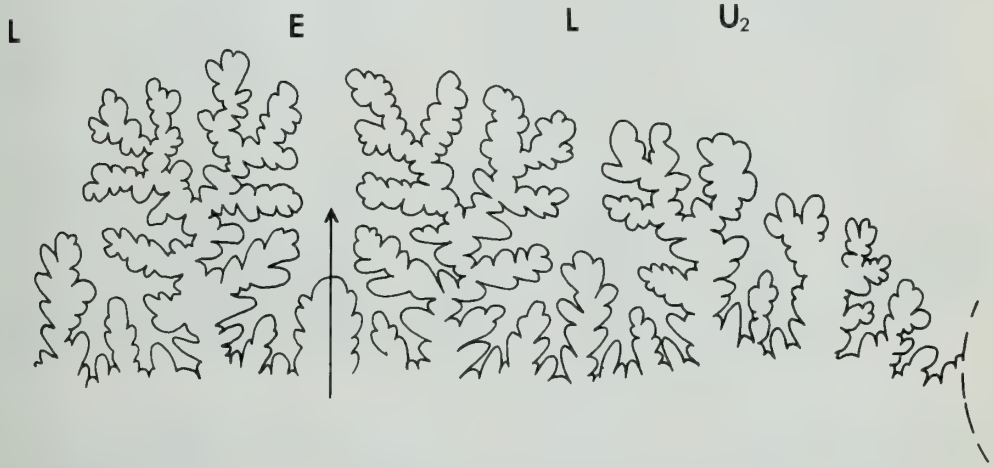


Fig. 2 External suture of *Anagaudryceras buddha* (Forbes). BM(NH) C78721, × 3½ approx.

These changes take place at different rates and at different diameters in different specimens, and spacing of constrictions is irregular; there is thus wide intraspecific variability.

Mature ornament, 50 mm onwards. Outer whorls and body chamber are ornamented by low, broad, straight, prorsiradiate to gently flexed band-like ribs separated by narrow furrows which are clearly derived from the constrictions present on early and middle growth stages. On the shell, the ribs are typically flattened, with a flattened apertural face so that they appear distinctly scale-like, whilst the whole shell surface bears fine lirae (Pl. 10, fig. 1). On the internal mould, ribs tend to be rounded and furrows broader than when shell is preserved.

Ornament is, however, enormously variable. In some specimens, close-spaced regular furrows give a *Kossmatella*-like appearance (Pl. 9, fig. 3); other individuals show very irregular ribs, with some broad segments of almost smooth whorl between constricted areas (Pl. 10, fig. 2).

Our specimens are adult at diameters of 90–100 mm, and typically show crowded, narrow flexed ribs over the last few centimetres immediately before the aperture, which is simple with a gently projected ventral peak.

The suture line (Fig. 2) is deeply incised with a lanceolate ventral lobe, a large, bifid, deeply-incised first lateral saddle (E/L), a smaller, bifid second lateral saddle (L/U_2), a bifid lateral lobe (L) which is shallower than the ventral lobe (E), and a retracted suspensive lobe with a large asymmetrically bifid first auxiliary lobe; the number of auxiliaries is not clear. The internal suture is not well exposed, but some specimens show a well-developed septal lobe.

DISCUSSION. Our collections are the largest known for this species; the presence of specimens with and without test, and at various ontogenetic stages, show that there is great intraspecific variability.

The problems of nomenclature associated with *A. buddha* stem from the description by Forbes (1846) of successive ontogenetic stages of the same species under different names, *Ammonites sacya* for the juvenile and *Ammonites buddha* for the adult. Our collections confirm the view that these are indeed synonymous, but contrary to common usage the name *buddha* has page priority, as Breistroffer (*in* Besairie 1936) has indicated.

There are a large number of names available for specimens at both the *sacya* and *buddha* stages, but we feel fairly confident that *Anagaudryceras limatum*, *A. limatum obscura*, *A. revelatum*, *A. utaturense*, *A. choffati*, *A. filicinctum*, '*Kossmatella*' *whitneyi*, '*Kossmatella*' *cappsi* and '*Murphyella*' *enigma* fall within the range of intraspecific variability. The Albian species *A.* ('*Paragaudryceras*') *sakalavum* (Collignon 1949 : 51; pl. 7, figs 3, 3a, 3b) differs from *A. buddha* in the subdued nature of the ornament of the outer whorls, together with differing proportions, which place it outside the range of variation seen in our material. It probably represents no more than the unornamented end member of variability within the species group. A further Albian species from Madagascar, *A.* ('*Paragaudryceras*') *coagmentatum* (Collignon 1963 : 20; pl. 249, fig. 1064) is probably a synonym of *A. buddha*. It was distinguished by Collignon on the basis of a proportionately lower (41% as opposed to 46%) and narrower (40% as opposed to 44%) whorl than in the present species, a larger umbilicus (37% as opposed to 29%) and strikingly scale-like ornament. The type specimen is a fragment only and retains its test; its ornament can be readily matched with portions of *buddha* variants in our collections. The same is probably true of the ill-preserved *A.* ('*Paragaudryceras*') *mokarahaense* (Collignon 1950 : 67; pl. 11, figs 1–2; pl. 12, fig. 5). *Anagaudryceras subsacya* (Marshall) (see Henderson 1970 : 18; pl. 2, figs 5, 6 and below) from the Campanian is a direct descendant of *A. buddha*. It shows a comparable style of ornament in early and mature stages,but the fold-like ribs of mature specimens appear to be consistently finer in *subsacya*. We therefore regard it as a distinct successional species, although noting that the type specimen of the Turonian–Coniacian *Anagaudryceras limatum intermedia* (Yabe) is morphologically intermediate, and that there may be a case for applying the name *Anagaudryceras intermedia* to Turonian and Coniacian forms if these are consistently different from earlier ones.

Anagaudryceras aurarium Anderson (1938 : 151; pl. 20, figs 1, 2; types refigured by Murphy 1967*b*) is a distinctive involute species, with distant constrictions and narrow collars when young, and with distant deep constrictions separating very broad flattened ribs when adult.

Other *Anagaudryceras* species either belong to the *involvulum* group, or are juveniles at the *sacya* stage. Most of these (see Collignon 1956 : 69, sections K, L for a fairly complete summary) are too poorly characterized for profitable discussion, and their relations to species known as adults is not determinable.

OCCURRENCE. Middle and Upper Albian of Zululand; Middle Albian, Cenomanian and Turonian of Madagascar, Cenomanian of Mozambique, Cenomanian of New Zealand, Cenomanian to Coniacian of Japan, Cenomanian of Alaska, Albian of British Columbia and California, Albian and Cenomanian of central and southern Europe, Albian of the Balkans.

Anagaudryceras subsacya (Marshall)

(Pl. 11, fig. 3)

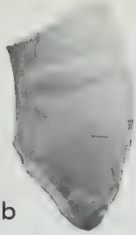
1917 *Lytoceras* sp. Marshall : 445; pl. 33, fig. 3; text-fig. 4.

Plate 12 × 1, except Figs 1c–d

Figs 1–3, 5–10 *Anagaudryceras pulchrum* (Crick). All Mzinene Formation, Albian V, Mzinene–Munywana areas, Zululand. Fig. 1, BM(NH) C78782, Bed 12 or 13, Loc. 51: × 2 in figs 1c–d to show details of lirae and collars. Fig. 2, BM(NH) C78815, Loc. 65; Fig. 3, BM(NH) C78797, Bed 12, Loc. 51; Fig. 5, SAS 56, Loc. 51; Fig. 6, BM(NH) C78781, Bed 9 or 10, Loc. 51; Fig. 7, BM(NH) C78793, Bed 12, Loc. 51; Fig. 8, BM(NH) C78818, Loc. 66; Fig. 9, BM(NH) C78774, Bed 6, Loc. 51; Fig. 10, BM(NH) C78796, Bed 12, Loc. 51. See also Pl. 6, figs 3–4; Pl. 13.

Figs 4, 11 '*Gaudryceras*' spp. Fig. 4, BM(NH) C18271; Fig. 11, BM(NH) C18269. Specimens mentioned by Crick (1907*b* : 238, 239), from Munywana Creek; presumably Albian.

1a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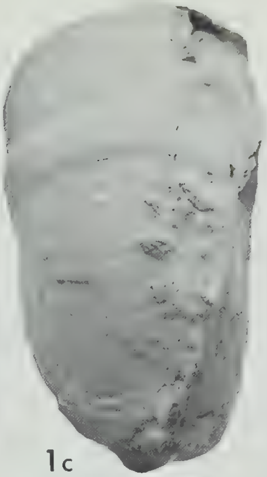
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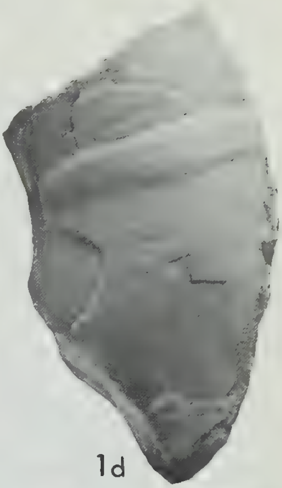
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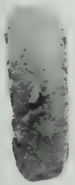
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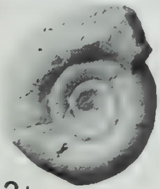
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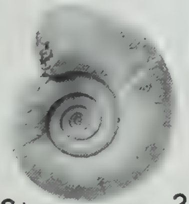
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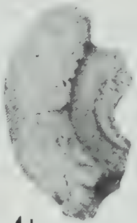
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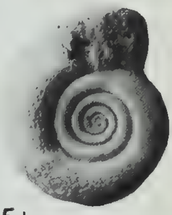
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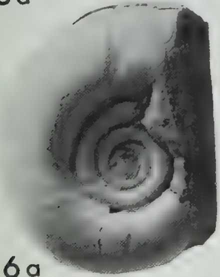
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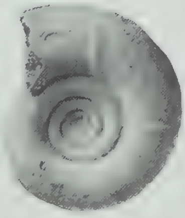
7a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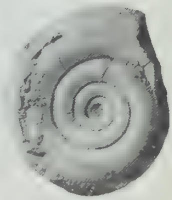
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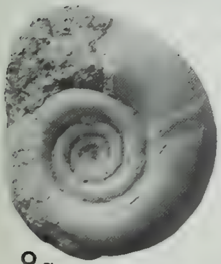
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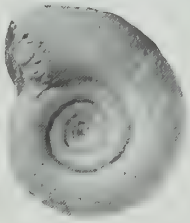
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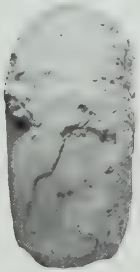
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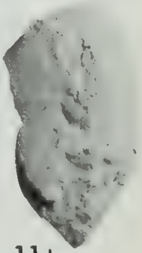
11b

1926 *Gaudryceras subsacya* Marshall: 144; pl. 20, figs 8–9; pl. 29, figs 1–2.
1965 *Anagaudryceras subsacya* (Marshall) Howarth: 358.
1970 *Anagaudryceras subsacya* (Marshall); Henderson: 18; pl. 2, figs 5–6; text-fig. 5a.
1972 *Anagaudryceras subsacya* (Marshall); Kennedy, Kauffman & Klinger: 100; pl. 3, figs 1a–b.

LECTOTYPE. Designated by Henderson (1970: 18), the original of Marshall 1926: pl. 29, figs 1–2, from the Mata Series of North Auckland, New Zealand, and probably of Lower–Middle Campanian age.

MATERIAL. Two specimens, UND 6545 and 6546 from the Umzamba Formation at Loc. 4, Sometsu Road, Durban, and of Santonian or Campanian age.

DESCRIPTION. Our best-preserved specimen is an internal mould, too fragmentary for measurement. The coiling is evolute, with an evenly-rounded whorl section, depressed (whorl breadth/height ratio up to 1·33) when young, becoming progressively less depressed as diameter increases (ratio decreases to almost 1·0). The expansion rate is moderately high. The umbilicus is broad, up to 45% of diameter when young, falling to just over 30% when adult, and shallow. As in *Anagaudryceras buddha*, two distinct types of ornament are present. Up to a diameter of about 40 mm, the test bears fine, dense striae which sweep gently forwards across flanks and venter, as do periodic collar-like ribs, five per whorl, in front of each of which is a narrow, shallow constriction. The mould is smooth, save for subdued collars and rather more conspicuous constrictions. On the mould of the body chamber, ornament consists of fine, irregular, narrow, band-like ribs separated by shallow, rounded furrows. The ribs are gently flexed on the flanks and slightly projected on the venter. The transition zone between the two types of ornament is not fully preserved.

The suture line is incompletely exposed, but includes a long, moderately subdivided, lanceolate ventral lobe, a large, deeply-incised bifid first lateral saddle (E/L), and a smaller, ? bifid second lateral saddle (L/U_2). The suspensive lobe is strongly retracted, with at least three auxiliary lobes, the first large and asymmetrically bifid.

DISCUSSION. As noted above, the species with which *Anagaudryceras subsacya* shows closest similarities is *Anagaudryceras buddha*, from which it is descended. The inner whorls of the two species are virtually identical, but with the appearance of adult ornament, the band-like ribs of *subsacya* appear to be consistently finer and more regular than those of *buddha*.

OCCURRENCE. Lower to Middle Campanian of New Zealand, Santonian/Campanian of Durban, Natal.

Anagaudryceras politissimum (Kossmat)
(Pl. 5, fig. 3)

1895 *Lytoceras* (*Gaudryceras*) *politissimum* Kossmat: 128; pl. 15, figs 7a–c.
non 1909 *Gaudryceras politissimum* Kossmat; Kilian & Reboul: 14; pl. 1, figs 7, 8.
? 1926 *Gaudryceras politissimum* Kossmat; Marshall: 145; pl. 28, figs 1, 3; text-fig. 3 (= *Anagaudryceras particostatum* Marshall according to Henderson 1970: 17).
non 1938 *Gaudryceras politissimum* Kossmat; Collignon: 42; pl. 7, figs 2–2a (= *Anagaudryceras mikobokoense* Collignon).
1956 *Anagaudryceras politissimum* (Kossmat); Collignon: 58; pl. 8, figs 2a–c.

HOLOTYPE. Kossmat's original specimen from the Upper Trichinopoly group of Varagur, southern India.

MATERIAL. A single specimen, SAS H202/1, from the St Lucia Formation at Loc. 87, False Bay, Lake St Lucia, Zululand (Santonian I–II).

DIMENSIONS.	D	Wb		Wh		Wb/Wh	U	
Holotype (after Kossmat)	89	28	(31)	33	(37)	0·85	34	(38)
Collignon 1956: pl. 8, fig. 2	97	30	(31)	37	(38)	0·81	36	(37)

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
Collignon 1956 : 59	105	31 (30)	38 (36)	0·82	37 (35)
SAS H202/1	61·2	21·5 (35)	21·8 (36)	0·98	22·4 (37)
Anagaudryceras involvulum (after Stoliczka)	44·0	16·0 (36)	19·0 (43)	0·84	14·6 (30)
Anagaudryceras madraspatanum (after Stoliczka)	30	13 (43)	12·0 (40)	1·08	10·8 (36)
Anagaudryceras yamashitai (after Yabe)	88	33 (37)	44 (50)	0·75	22 (25)
Anagaudryceras mikobokoense (after Collignon)	92	35 (38)	39 (42)	0·9	35 (38)

DESCRIPTION. The coiling is relatively evolute, about 30% of the previous whorl being covered. The whorl section is slightly compressed (whorl breadth/whorl height ratio 0·98), the greatest breadth being some way below mid-flank. The umbilicus is fairly wide (37% of diameter), shallow, with a low rounded umbilical wall and shoulder which merge into the moderately inflated, rounded and convergent flanks. The ventrolateral shoulders are rounded, merging with an arched, rounded venter.

The shell surface is not well preserved in our specimen, but appears to have borne very fine, flexuous, prorsiradiate lirae, projected on the venter as a shallow broad peak. There appear to have been four or five flexuous, rounded collar-like ribs per whorl, parallel to the lirae, and followed by shallow constrictions.

The internal mould is smooth, save for the low collar-like ribs and constrictions. The suture line is poorly visible, but is made up of moderately incised, bifid lobes and saddles.

DISCUSSION. As Howarth (1965, 1966) has noted, the second species group recognizable within *Anagaudryceras* listed above (p. 146) includes a large number of named forms based either on juveniles or geographically and stratigraphically isolated individuals. It is thus not at present possible to assess intraspecific variability nor to decide upon valid interspecific criteria, although it seems clear that *Anagaudryceras involvulum* (of which *A. utaturense* Shimizu is a synonym), *A. madraspatanum*, *A. yamashitai* and *A. mikobokoense* (of which *Gaudryceras aenigma* Haas and *G. aureum* Anderson are synonyms) can be differentiated from our specimen on the basis of differing relative proportions, as summarized in the table above. It is clearly distinguished from *Anagaudryceras pulchrum* and *A. subtilineatum*, discussed below, on similar criteria, whilst *A. particostatum* and *A. tennanti* are based on juveniles too small for proper comparison.

Our specimen thus finds its closest similarities with *Anagaudryceras politissimum* in terms of style of ornament and proportions, although less compressed than Kossmat's type.

OCCURRENCE. *Anagaudryceras politissimum* is known from the Turonian to Santonian of southern India, the Maastrichtian of Madagascar and the Santonian of Zululand.

***Anagaudryceras subtilineatum* (Kossmat)**
(Fig. 3; Pl. 14, figs 3, 12)

1895 *Lytoceras* (*Gaudryceras*) *subtilineatum* Kossmat : 123; pl. 10, figs 1a–c, 2a–b.
1921 *Gaudryceras tenuilineatum* van Hoepen : 5; pl. 2, figs 7–9; text-fig. 2.
? 1921*b* *Gaudryceras* sp. juv. Spath : 41.
1922 *Gaudryceras tenuilineatum* van Hoepen; Spath : 117.
1956 *Anagaudryceras subtilineatum* (Kossmat) Collignon : 68.
1956 *Gaudryceras tenuilineatum* van Hoepen; Collignon : 70.
1965 *Anagaudryceras subtilineatum* (Kossmat); Howarth : 358.

LECTOTYPE. Herein designated, the original of Kossmat 1895 : pl. 19, figs 1a–c, from the Arialoor Group of Karapady, southern India.

MATERIAL. We have five specimens, the holotype of *Gaudryceras tenuilineatum* TM 559, SAM 7036, a further two fragments in the Durban Museum (unregistered) and a doubtful fragment BM(NH) C78757, all from the late Santonian to early Campanian Umzamba Formation at Loc. 1, the mouth of the Umzamba River, southern Natal (Pondoland).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
TM 559	26·5	10·8 (41)	7·3 (28)	1·48	13·4 (51)

DESCRIPTION. The coiling is evolute, about 30% of the previous whorl being covered, the whorls expanding rather slowly. The whorl section is depressed, the greatest breadth being close to mid-flank. The umbilicus is broad (51% of diameter) and of moderate depth, with a rounded umbilical wall. The whorl section is depressed, evenly rounded, with a broad venter. The shell surface appears smooth to the naked eye, but is in fact covered in very fine, dense lirae. These arise at the umbilical seam, or from a point some way up the wall or flank. The lirae at first run normal to the umbilical seam, but sweep forwards across the umbilical shoulder and lower flank, are rectiradiate at mid-flank, and sweep forwards over the shoulder to produce a shallow, broad, ventral peak.

There are four shallow constrictions on the outer whorl; behind each is a low, rounded collar. Both rib and collar run parallel to the lirae and are themselves lirate.

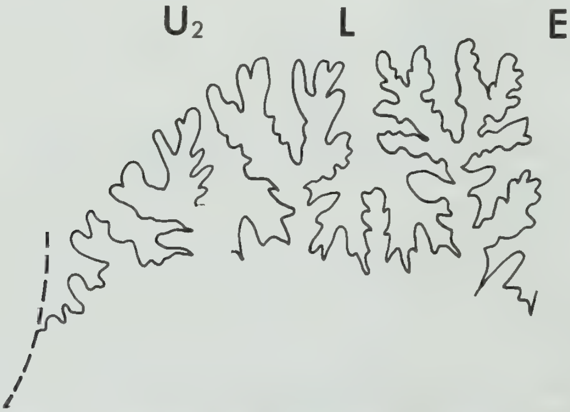

Fig. 3 External suture of *Anagaudryceras subtilineatum* (Kossmat). TM 559 (holotype of *Gaudryceras tenuilineatum* van Hoepen), × 7½ approx.

The suture (Fig. 3) consists of a quite deeply divided ventral lobe (E) with a lanceolate ventral saddle extending for half its height, a large, bifid first lateral saddle (E/L) and a smaller bifid second lateral saddle (L/U_2), a lateral lobe (L) which is symmetrically bifid and shallower than the ventral lobe, plus a retracted suspensive lobe with bifid auxiliaries.

DISCUSSION. *Anagaudryceras subtilineatum* is a poorly-known species, being based upon a large fragment of an individual with a maximum whorl height of 24 mm and a septate nucleus only 25 mm in diameter. The fine ornament indicates, however, that it is clearly an *Anagaudryceras*.

Van Hoepen (1921) separated his *Gaudryceras tenuilineatum* from Kossmat's species on the basis of slightly differing relative proportions. The figures of Kossmat show, however, that proportions vary enormously with age, whilst the identical ornament of the two groups of specimens leads us to place them in synonymy.

The evolute coiling, depressed whorl section, fine ornament and limited number of constrictions serve to distinguish *Anagaudryceras subtilineatum* from species such as *A.* '*sacya*' and *subsacya* at comparable diameters, and from *A. mikobokoense*, *A. politissimum*, *A. madraspatanum*, *A. involvulum*, *A. yamashitai* and *A. tennanti* at large diameters. The closest comparisons are clearly with *Anagaudryceras pulchrum*, but in this Albian species the umbilicus is proportionally smaller, the expansion rate greater, the ornament coarser and the constrictions and collar ribs more conspicuous.

Occurrence. Campanian? of southern India, Santonian or Campanian of southern Natal (Pondoland).

Anagaudryceras pulchrum (Crick)

(Fig. 4; Pl. 6, figs 3, 4; Pl. 12, figs 1–3, 5–10; Pl. 13, figs 1–9)

1907*b* *Gaudryceras pulchrum* Crick: 237; pl. 15, figs 1, 1a.
1936 *Lytoceras* (*Gaudryceras*) *sacya* (Forbes); Venzo: 78; pl. 5, figs 8a–b; pl. 6, figs 5a–b.
1956 *Anagaudryceras pulchrum* (Crick) Collignon: 68.
1964 *Anagaudryceras pulvinatum* (Crick); Collignon: 30; pl. 324, fig. 1445.

Holotype. BM(NH) C18266 from the 'south branch of the Manuan Creek, Zululand', figured by Crick (1907*b*: pl. 15, figs 1–1a), and of Upper Albian age.

Material. In addition to the holotype, there are two paratypes, BM(NH) C18267–8, also from the Munywana, and a large number of additional specimens. SAS GSO 1–4, SAS 55–57, A3056, A3061–2 and SAS U1–3 are from the Mzinene Formation at Loc. 51 (Albian IV–V, precise horizon unknown); BM(NH) C78774–5 are from Bed 6, C78776–7, C78779–80 from Bed 8, C78781–3 from Beds 9 or 10, C78784 from Bed 10 or 11, C78785–78797 from Bed 12, C78799–78801 from Bed 12 or 13 at the same locality (Albian V); BM(NH) C78802 from Loc. 52, BM(NH) C78803–13 from Loc. 54 (Albian V), BM(NH) C78816, C78820–2 from Loc. 56 (Albian V), all on the Mzinene. BM(NH) C78814 is from Bed 4 of the Mzinene Formation at Loc. 64, C78815 from Loc. 65 and C78817–9 from Loc. 66, all Mzinene Formation (Albian V) on the Munywana and its tributaries.

Dimensions.	*D*	*Wb*	*Wh*	*Wb*/*Wh*	*U*
Paratype, BM(NH) C18268	21·8	9·9 (45)	6·5 (30)	1·52	10·4 (48)
Paratype, BM(NH) C18267	34·8	14·5 (41)	11·0 (32)	1·32	15·5 (45)
Holotype, BM(NH) C18266	39·0	15·5 (38)	12·5 (32)	1·24	16·8 (43)
BM(NH) C78797	27·3	11·3 (41)	9.3 (34)	1·22	12·0 (44)
BM(NH) C78793	29·0	11·8 (41)	10·8 (37)	1·1	13·2 (45)
BM(NH) C78794	30·3	12·7 (42)	10·0 (33)	1·27	14·0 (46)
BM(NH) C78802	44·4	16·7 (38)	15·7 (35)	1·06	17·3 (39)
BM(NH) C78776	48·2	–	17·2 (36)	–	19·2 (40)

Description. The coiling is very evolute, slowly expanding, with a broad shallow umbilicus. The umbilical wall is low and slopes outwards, merging with the inflated flanks. The whorl section is depressed at first (whorl breadth/height ratio 1·5–1·3), but as diameter increases the whorls become less depressed, and eventually almost as broad as high. The venter, initially rather flattened, becomes first broadly rounded, and then somewhat arched. When well preserved, the surface of the test is covered in fine dense striae. These arise at the umbilical seam, pass slightly forwards across the wall and shoulder, and are distinctly prorsiradiate on the flanks, where they are gently flexed, forwards to mid-flank, backwards across the upper flank, thence passing across the venter with the shallowest of ventral peaks.

There are four or five collar ribs and associated constrictions per whorl during the early growth stages, increasing to seven or more when fully grown. These collars are parallel to the lirae, and have a gently rounded apical slope and a steep, abrupt apertural slope, giving them a distinctly scale-like appearance. The constrictions are narrow, and both collar and constriction are lirate.

The internal mould is smooth, save for periodic collars and constrictions which are broader and shallower than on the test.

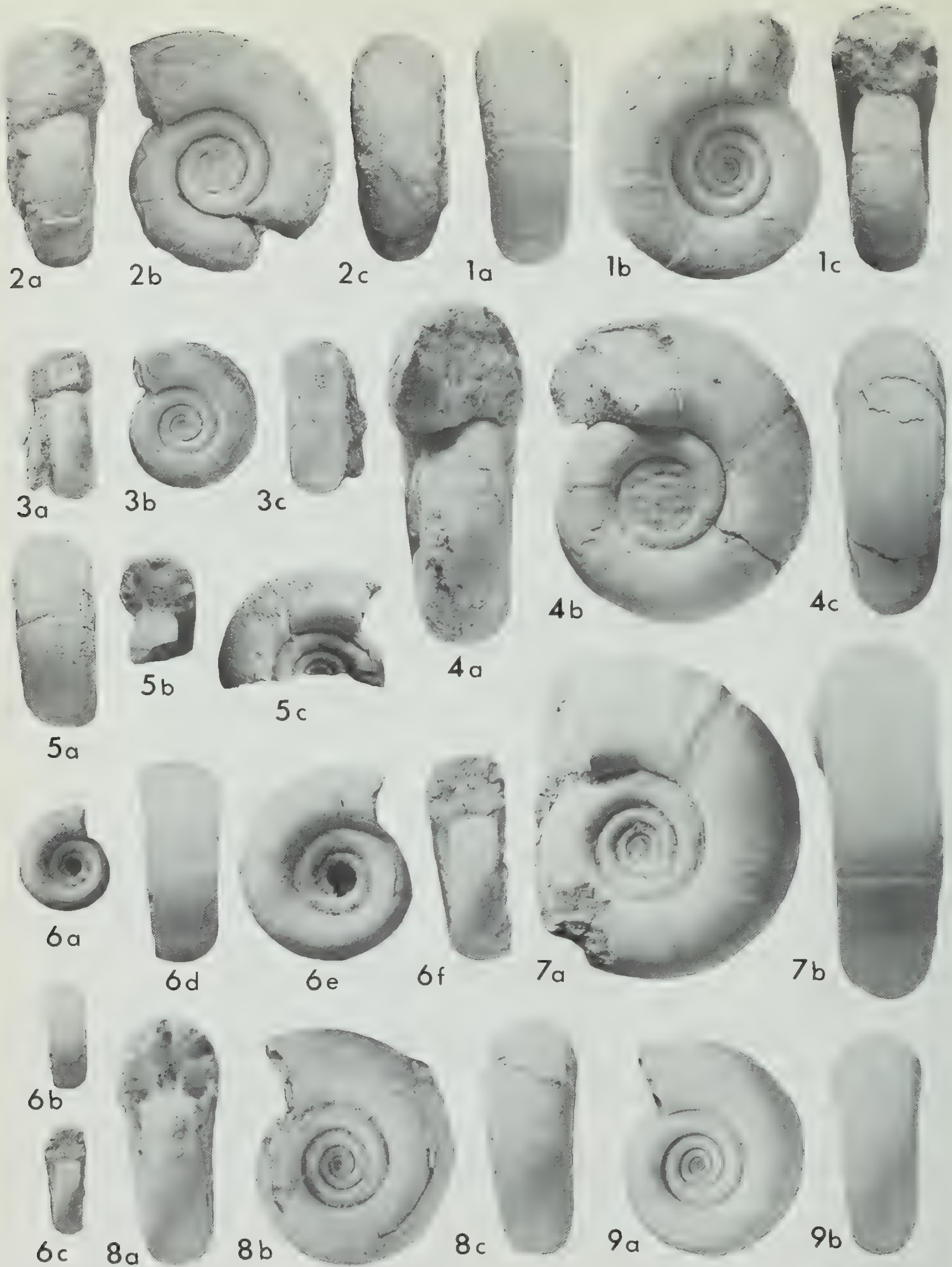
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Plate 13 ×1, except Figs 6d–f

Figs 1–9 *Anagaudryceras pulchrum* (Crick). All from Mzinene Formation, Albian V, Mzinene–Munywana area, Zululand. Fig. 1, the **holotype,** BM(NH) C18266; Fig. 2, paratype, BM(NH) C18267; Fig. 3, paratype, BM(NH) C18268; Fig. 4, BM(NH) C78802, Loc. 52; Fig. 5, BM(NH) C78816, Loc. 56; Fig. 6, BM(NH) C78783, Bed 9 or 10, Loc. 51, Figs 6d–f ×2 to show juvenile features; Fig. 7, BM(NH) C78776, Bed 8, Loc. 51; Fig. 8, SAS VI and Fig. 9, SAS A55, both Loc. 51 (precise horizon unknown), Fig. 8 showing a well-preserved septal lobe. See also Pl. 6, figs 3–4; Pl. 12, figs 1–3, 5–10.

The suture (Fig. 4) consists of a large, moderately incised, bifid ventral lobe (E) with a narrow lanceolate ventral saddle extending to half its height, a large bifid first lateral saddle (E/L) and a smaller second lateral saddle (L/U_2), both symmetrically bifid, and separated by a bifid lateral lobe (L) with a large, slender central foliole. The suspensive lobe is retracted, with five auxiliary saddles, the first large and asymmetrically bifid. There is a deep and narrow internal lateral lobe (I) flanked by a large lateral saddle, and a large, horseshoe-shaped septal lobe.

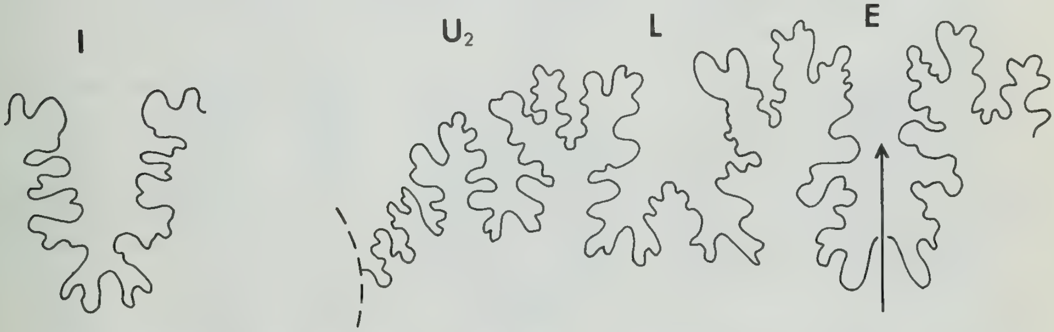


Fig. 4 External and internal sutures of *Anagaudryceras pulchrum* (Crick). SAS 56, ×7 approx.

DISCUSSION. *Anagaudryceras pulchrum* closely resembles *A. buddha* when young, but the two species can be separated on the basis of the coarser lirae of *pulchrum*, scale-like collars, less depressed whorl section and more evolute coiling. Adults of the two species are clearly distinguished by the fold-like ribs of *buddha*. *Anagaudryceras subtilineatum*, a close ally from a somewhat higher horizon, appears to be more depressed when young and to possess more markedly flexed lirae; it bears the same relationship to *A. pulchrum* as *Anagaudryceras subsacya* does to *A. buddha*.

Gaudryceras pulvinatum Collignon (1964 : 30; pl. 324, fig. 1445) was separated from *Anagaudryceras pulchrum* on the basis of its Cenomanian age and differing proportions (at 48 mm diameter, $Wb = 40\%$, $Wh = 40\%$, $U = 31\%$), plus a change from a depressed to a compressed whorl section as diameter increases and a consequent decrease in proportionate umbilical width; it is best regarded as a synonym of *A. pulchrum*.

Anagaudryceras cassisianum (d'Orbigny 1850), from Cassis in the south of France, appears to be a close relation of *A. pulchrum*. From the figures of Fabre (1940 : 15; pl. 5, figs 8, 9) this species seems to have a smaller umbilicus than *pulchrum* at comparable diameters (30% as opposed to over 40%), slowly expanding whorls which are strikingly depressed when young, more prominent lirae, and scale-like collars. More material is needed to determine its true affinities.

OCCURRENCE. Upper Albian of Zululand; Lower Cenomanian of Madagascar.

Genus *VERTEBRITES* Marshall, 1926

TYPE SPECIES. *Vertebrites murdochi* Marshall 1926.

DIAGNOSIS. Very evolute, many-whorled serpenticone gaudryceratids retaining a depressed, subrectangular whorl section throughout ontogeny. Ornament consists of fine prorsiradiate lirae which are simple and rather prominent on the flank, dividing into many finer lirae over the venter. Internal suture with several saddles which increase in size from the dorsal lobe towards the umbilical seam.

DISCUSSION. Treatment of *Vertebrites* has varied from its acceptance as merely a subgenus of *Gaudryceras* (Matsumoto 1959*a*) to separation as the sole member of a subfamily Vertebritinae (Wiedmann 1962*a*), on the basis of the presence of a greater number of umbilical lobes than in the

Gaudryceratinae *sensu stricto*. Henderson (1970 : 22) noted, however, that forms such as *Anagaudryceras tennanti* Henderson (1970 : 19; pl. 2, figs 4, 7; text-fig. 5b) and *Gaudryceras varicostatum* (van Hoepen) (= *Anagaudryceras subtilineatum* Kossmat) are transitional to *Vertebrites* in shell form and proliferation of umbilical lobes, whilst Matsumoto (1959*a* : 141) noted that some juvenile *Gaudryceras*, *sensu stricto*, e.g. *Gaudryceras tenuiliratum* Yabe, resemble *Vertebrites* in both shell form and ornament. We would also draw comparisons to juveniles of *Gaudryceras stefaninii* and *G. varicostatum* described and figured here (Pl. 1, figs 2, 8; Pl. 3, figs 3a-d) in this respect. We have followed a conservative course, and treat *Vertebrites* as an independent genus.

The only form likely to be confused with *Vertebrites* is *Gaudryceras, sensu stricto*, and the larger size of this genus when mature, its wire-like ornament in typical members and the nature of the constrictions and suture make confusion unlikely.

The following species are currently referred to the genus. *Vertebrites kayei* (Forbes 1846 :101; pl. 8, fig. 3), Santonian, Campanian and Maastrichtian. *Vertebrites murdochi* (Marshall 1926 : 139; pl. 20, figs 9, 9a; pl. 30, figs 1, 2; pl. 40, fig. 3), Campanian.

Occurrence. *Vertebrites* ranges from the Santonian to Lower Maastrichtian, and its geographical distribution extends to southern India, Japan, New Caledonia, New Zealand, Madagascar, South Africa (Zululand and Pondoland), Chile, Texas and northern Mexico, California, Tunisia and Belgium.

Vertebrites kayei (Forbes)
(Fig. 5; Pl. 14, fig. 2)

1846 *Ammonites kayei* Forbes : 101; pl. 8, fig. 3.
1865 *Ammonites kayei* Forbes; Stoliczka : 156; pl. 87, figs 1, 1a.
1871 *Lytoceras kayei* (Forbes) Griesbach : 63.
1895 *Lytoceras* (*Gaudryceras*) *kayei* (Forbes); Kossmat : 124, 162; pl. 16, figs 5a–b; pl. 17, figs 2a–b.
1895 *Lytoceras kayei* (Forbes); Steinmann : 86; pl. 15, figs 5a–b; text-fig. 8.
1906 *Gaudryceras kayei* (Forbes); Woods : 335; pl. 41, fig. 8; pl. 42, fig. 1.
1907 *Lytoceras* (*Gaudryceras*) *kayei* (Forbes); Pervinquière : 69; pl. 3, figs 2a–b.
? 1908 *Gaudryceras kayei* (Forbes); de Grossouvre : 34; pl. 9, fig. 4.
1927 *Gaudryceras kayei* (Forbes); Böse : 269; pl. 10, figs 10–14; pl. 11, figs 5–10.
1956 *Vertebrites kayei* (Forbes) Collignon : 64; pl. 6, figs 4a–c.
? 1958 *Lytoceras* (*Gaudryceras*) *kayei* (Forbes); Anderson : 182.

Plate 14 × 1, except Figs 6d–e

Fig. 1 *Zelandites* sp. 2. SAM 7100, late Santonian or early Campanian Umzamba Formation, Loc. 1, mouth of Umzamba River, southern Natal (Pondoland).

Fig. 2 *Vertebrites kayei* (Forbes). BM(NH) C78756, St Lucia Formation (Campanian), Loc. 14, Mfolozi River, Zululand.

Figs 3, 12 *Anagaudryceras subtilineatum* (Kossmat). Fig. 3, SAM 7036; Fig. 12, TM 559, holotype of *Gaudryceras tenuilineatum* van Hoepen; both from late Santonian to early Campanian Umzamba Formation, Loc. 1, mouth of Umzamba River, southern Natal (Pondoland).

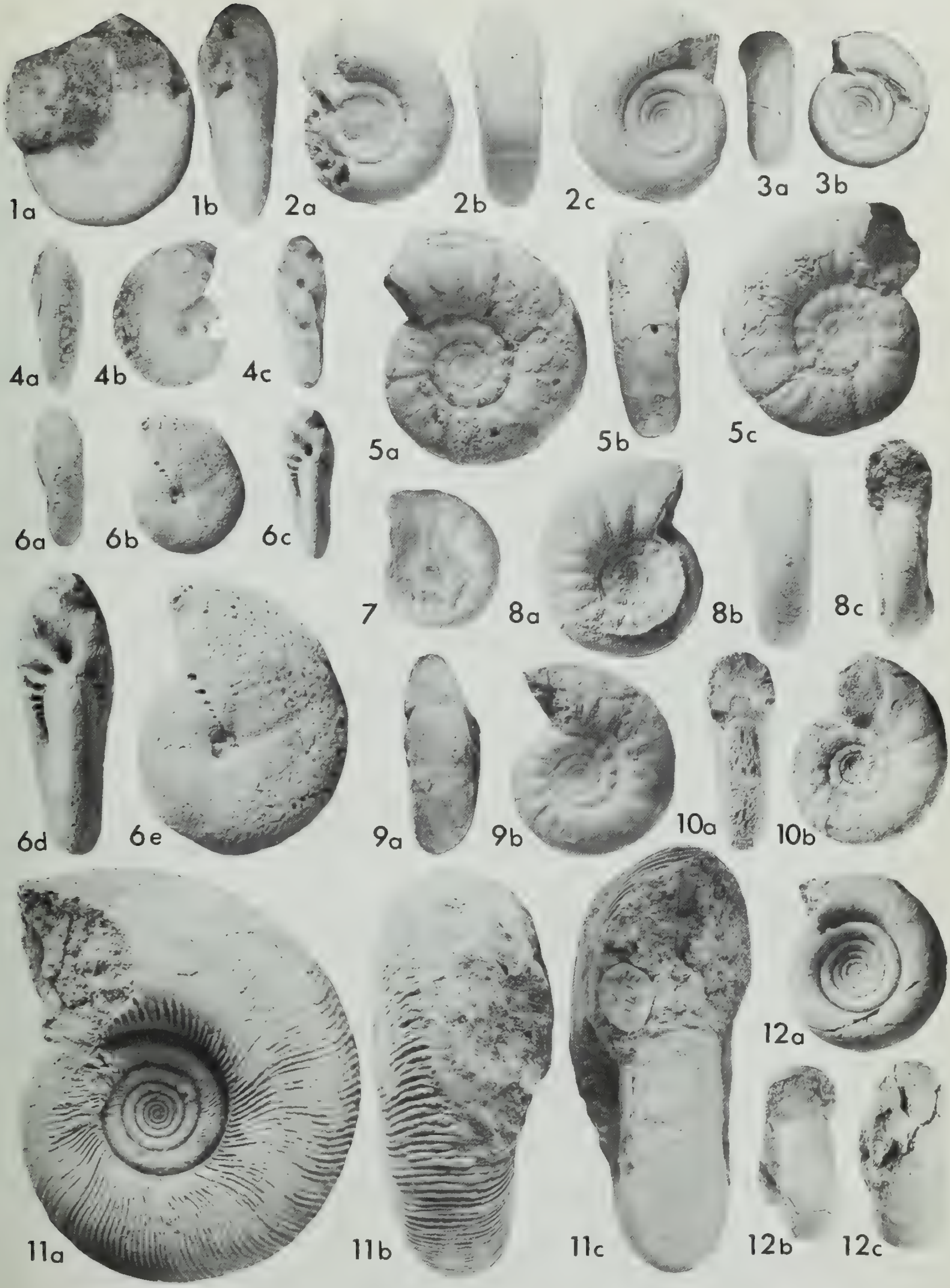
Fig. 4 *Zelandites odiensis* (Kossmat). BM(NH) C18141, Lower or Middle Cenomanian Mzinene Formation, Skoenberg area, Mzinene River, Zululand.

Figs 5, 7, 9, 10 *Kossmatella* (*Kossmatella*) aff. *romana* Wiedmann. Fig. 5, BM(NH) C78764; Fig. 7, SAS Z539b; Fig. 9, BM(NH) C78763; Fig. 10, SAS Z539a; all from Mzinene Formation, Albian V, Loc. 56, Mzinene River, Zululand.

Fig. 6 *Zelandites* sp. 1. BM(NH) C78864, Mzinene Formation, Middle Cenomanian, Loc. 62, the Skoenberg, Zululand, Figs 6d–e × 2 to show constrictions.

Fig. 8 *Kossmatella* (*Kossmatella*) *marut* (Stoliczka). BM(NH) C78762, Bed 12, Mzinene Formation, Albian V, Loc. 51, Mzinene River, Zululand.

Fig. 11 *Gaudryceras varicostatum* van Hoepen. Holotype of *Gaudryceras cinctum* Spath, BM(NH) C19415, late Santonian to early Campanian Umzamba Formation, Loc. 1, mouth of Umzamba River, southern Natal (Pondoland). See also Pls 3, 4; Pl. 7, fig. 2.


1a
1b
2a
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7
8a
8b
8c
6d
6e
9a
9b
10a
10b
11a
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11c
12a
12b
12c

1958 *Lytoceras (Gaudryceras) coalingense* Anderson : 184; pl. 68, fig. 1.
1958 *Lytoceras (Gaudryceras) birkhaueseri* Anderson : 185; pl. 68, figs 4–4a.
1959*a* *Vertebrites kayei* (Forbes); Matsumoto : 141, 142, 145.
1970 *Vertebrites kayei* (Forbes); Henderson : 22.

LECTOTYPE. Herein designated, Forbes' original specimen (1846 : pl. 8, fig. 3), BM(NH) C51050 from the Valudayar Group of Pondicherry, southern India.

MATERIAL. A single specimen, BM(NH) C78756, from the St Lucia Formation at Loc. 14 on the Mfolozi River, Zululand (Campanian). Woods (1906) records four specimens from the Umzamba Formation at Loc. 1, the mouth of the Umzamba River, southern Natal (Pondoland).

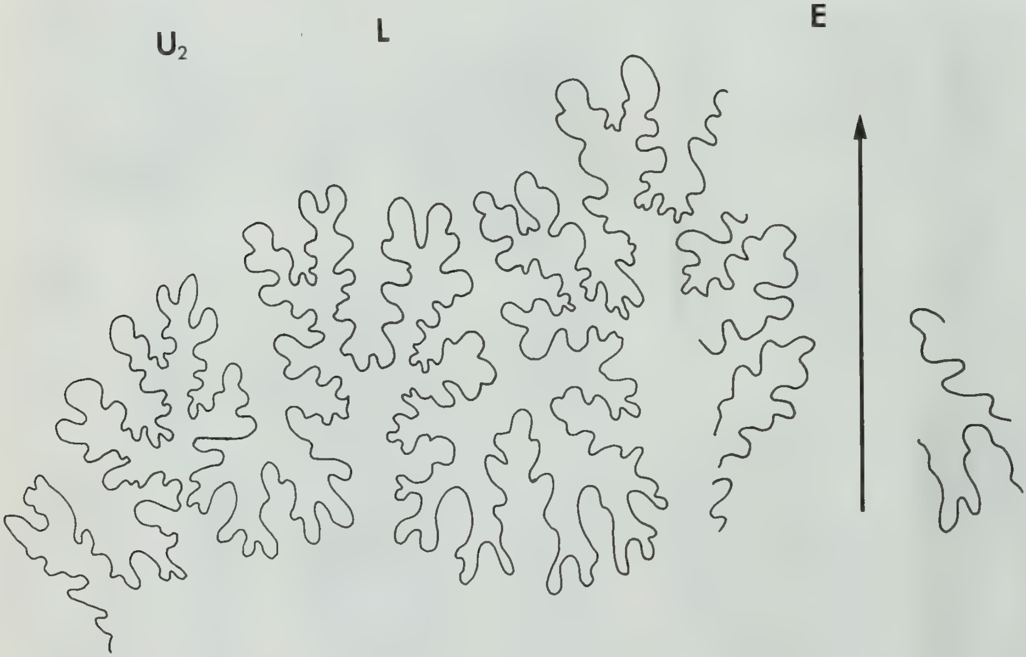

Fig. 5 External suture of *Vertebrites kayei* (Forbes). BM(NH) C78756, × 15 approx.

DESCRIPTION. The coiling is very evolute, with a slightly depressed, rounded to subrectangular whorl section, the greatest breadth being some way below mid-flank. The umbilicus is large (approximately 50% of diameter), shallow, with a low, rounded wall which merges into broad, rounded flanks. The ventrolateral shoulders are somewhat abruptly rounded, the venter broad and rather flattened. Ornament consists of fine, dense lirae which arise at the umbilical seam, sweep forwards over the umbilical wall and shoulder, and are straight and markedly prorsiradiate on the inner flanks. At about mid-flank they subdivide into numerous fine dense striae, almost invisible to the naked eye, and these flex gently backwards over the upper flank and then forwards over the ventrolateral shoulder to form a distinct peaked projection over the siphonal area.

There are periodic narrow, rounded collar-like ribs associated with narrow but distinct constrictions which are parallel to the lirae.

The internal mould is almost smooth save for shallow constrictions of which there are at least four on the outer whorl. The suture (Fig. 5) consists of a long, little subdivided, lanceolate ventral saddle, a large, highly subdivided asymmetrically bifid first lateral saddle (E/L) and a smaller, less irregularly bifid second lateral saddle (L/U_2). The ventral (E) and lateral lobe (L) are of the same length, the latter being bifid. There are three distinct auxiliaries on a retracted suspensive lobe. The first and largest auxiliary saddle is subtrifid.

DISCUSSION. *Vertebrites kayei* can be readily separated from the type species, *Vertebrites murdochi*, in that the latter species is consistently more depressed at corresponding growth stages (e.g. Henderson 1970 : 22; pl. 3, fig. 1; text-fig. 5c), the whorl breadth/height ratio being up to 2·25.

OCCURRENCE. This species is known from the Campanian of Zululand and the Santonian–Campanian of Pondoland. The type material, from southern India, is of Campanian age, although Kossmat (1895 : 86) records the species from Upper Santonian to Maastrichtian strata. In Chile, Texas, northern Mexico and perhaps Belgium, it occurs in the Lower Maastrichtian; Californian occurrences are of Upper Campanian to Maastrichtian age whilst there are records from the Santonian of Tunisia and an unspecified horizon in Japan.

Genus *ZELANDITES* Marshall, 1926

TYPE SPECIES. *Zelandites kaiparaensis* Marshall 1926.

SYNONYMY. *Varunaites* Shimizu, 1926 (type species *Ammonites varuna* Forbes 1846, by original designation); *Hypogaudryceras* Shimizu, 1934 (type species *Desmoceras kawanoi* Jimbo 1894, by monotypy); *Anazelandites* Matsumoto, 1938 (type species *Lytoceras* (*Gaudryceras*) *flicki* Pervinquière 1907, by original designation).

DIAGNOSIS. Small, typically rather involute gaudryceratids, inner whorls with a rounded cross-section, but becoming compressed and high-whorled, typically with a high, arched venter when adult. Shell surface may be ornamented by fine lirae, whilst the mould bears weak to strong, straight or sinuous constrictions, the position of which may be visible on the shell exterior. Suture line with a very asymmetrical first lateral lobe (E/L) in adults.

DISCUSSION. Eleven species or varieties of *Zelandites* are listed by Collignon (1956), to which can be added *Zelandites befamontensis* Collignon (1963 : 24; pl. 250, fig. 1075) from the Albian of Madagascar, *Zelandites dozei* (Fallot) *schroederi* Wiedmann (1962*a* : 161; pl. 8, figs 12, 13; pl. 13, figs 3, 4; text-figs 18–20) from the Middle Albian of Navarra, Spain and Sardinia, *Zelandites inflatus* Matsumoto (1959*b* : 74; pl. 23, figs 2a–d, 3a–c, 4a–c, 5a–d; pl. 24, figs 1a–c; text-fig. 14) from the Cenomanian of Japan and Albian of Alaska and *Zelandites perezi* McLearn (1972 : 40; pl. 37, fig. 1) from the Albian of British Columbia.

The only gaudryceratid genus likely to be confused with *Zelandites* is *Mesogaudryceras* Spath, 1927 (type species *Ammonites leptonema* Sharpe 1855). This genus has distinct but fine flexuous lirae, lacking in *Zelandites*, and is quite without constrictions.

OCCURRENCE. *Zelandites* is known to range from the Lower Albian to Lower Maastrichtian, and its distribution extends from northern Spain, southern France, the Balearics, Sardinia and north Africa to South Africa (Zululand), Madagascar, southern India, Japan, California, British Columbia, Alaska, New Zealand and Chile.

Zelandites odiensis (Kossmat)
(Pl. 14, fig. 4)

1865 *Ammonites varuna* Forbes; Stoliczka : 111; pl. 58, fig. 1.
1895 *Lytoceras* (*Gaudryceras*) *odiense* Kossmat : 129; pl. 18, fig. 1; pl. 19, fig. 3.
1907*a* *Gaudryceras odiense* Kossmat; Crick : 171; pl. 10, figs 14–14a.
1938 *Zelandites odiensis* (Kossmat) Matsumoto : 140, 141.
? 1942 *Zelandites odiensis* (Kossmat) *japonica* Matsumoto : 666 (*nomen nudum*).
1956 *Zelandites odiensis* (Kossmat); Collignon : 66.
1963 *Zelandites odiensis* (Kossmat); Collignon : 20; pl. 249, fig. 1066.

HOLOTYPE. By monotypy, Kossmat's original specimen (= *Ammonites varuna* Stoliczka (*non* Forbes) 1865 : pl. 58, fig. 1) from the Utatur group of Odium, southern India, and probably of Cenomanian age.

MATERIAL. A single specimen in William Anderson's collection, BM(NH) C18141, clearly from the Mzinene Formation of the Skoenberg area of Zululand and of Lower to Middle Cenomanian age.

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
Holotype (after Kossmat)	19	6·4 (34)	8·5 (45)	0·75	4·5 (24)
BM(NH) C18141	22·3	7·2 (32)	11·0 (49)	0·65	4·0 (17)
Collignon 1963 : 20	38	14 (37)	17 (45)	0·82	11 (29)

DESCRIPTION. The coiling is involute, with a small, deep, conical umbilicus (17% of diameter). The whorl section is compressed (whorl breadth/height ratio 0·65), with the greatest breadth close to mid-flank. The umbilical wall slopes outwards, to merge with the broadly rounded, flattened flanks, which converge to the high, rather narrow, arched venter. The specimen retains corroded test, and none of the original ornament remains, nor are any constrictions visible. The suture is not exposed.

DISCUSSION. Our specimen is poorly preserved, but the involute coiling, compressed whorl section with greatest breadth at mid-flank, and lack of constrictions and lirae clearly place it in Kossmat's species. *Zelandites odiensis* may be separated from other members of the genus as follows.

Z. dozei (Fallot 1885 : 235; pl. 4, figs 3–3b) from the Albian to Cenomanian of France, Spain, Sardinia, Japan and Madagascar is a more evolute, inflated species, and bears distinct constrictions, as does *Z. dozei schroederi* Wiedmann (1962*a* : 161; pl. 8, figs 12, 13; pl. 13, figs 3, 4; text-figs 18–20), an Upper Albian species from Spain and Sardinia, which also has an almost trigonal whorl section. *Z. flicki* (Pervinquière 1907 : 65; pl. 3, fig. 16) from the Upper Albian of Tunisia is more evolute, and has closely-spaced prorsiradiate constrictions which are very prominent across the lower flank. *Z. befamontensis* Collignon (1963 : 24; pl. 250, fig. 1074) from the Lower Albian of Madagascar is a less compressed species (whorl breadth/height ratio 0·92) with a subtrigonal whorl section and weak, distant constrictions. *Z. busnardoi* Collignon (1956 : 62; pl. 6, figs 4–4a; text-figs 10–11) from the Santonian of Madagascar has subparallel flanks, is more evolute, and bears strong constrictions. *Z. kaiparaensis* Marshall (1926 : 147; pl. 19, figs 9–9a; pl. 31, fig. 12; Henderson 1970 : 21; pl. 2, fig. 8) from the Campanian of New Zealand and California is more inflated, with strong prorsiradiate constrictions. The presence of constrictions also serves to distinguish *Z. mihoensis* Matsumoto (1938 : 144; pl. 14, figs 2a–c) from the Cenomanian of Japan; *Z. inflatus* Matsumoto (1959*b* : 74; pl. 23, figs 2a–d, 3a–c, 4a–c, 5a–d; pl. 24, figs 1a–c; text-fig. 14) from the Albian of Alaska and Cenomanian of Japan, and *Z. kawanoi* (Jimbo 1894 : 281; pl. 1, fig. 7) from the Santonian to Maastrichtian of Japan.

Zelandites varuna (Forbes 1846 : 107; pl. 8, figs 5a–c) and *Z. varuna japonica* Matsumoto (1938 : 140; pl. 14, figs 5a–b, 6a–b, 7a–b; text-fig. 1a–d) from the Campanian–Maastrichtian of southern India, Japan and Chile (Steinmann 1895 : 84; pl. 5, figs 2a–b; text-fig. 7) are perhaps the most closely comparable species, but in these forms the greatest whorl breadth is closer to the umbilicus, whilst there are distinct lirae and constrictions which are particularly well marked on the lower flank.

OCCURRENCE. Cenomanian of southern India and South Africa (Zululand); Albian of Madagascar, and perhaps Cenomanian of Japan (Matsumoto 1942).

Zelandites sp. 1

(Pl. 14, fig. 6)

MATERIAL. A single specimen, BM(NH) C78864, from the Middle Cenomanian Mzinene Formation at Loc. 62, the Skoenberg, Zululand.

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
BM(NH) C78864	21·5	12·1 (56)	11·5 (53)	1·05	2·0 (9)

DESCRIPTION AND DISCUSSION. This corroded specimen from the same general locality as the specimen of *Zelandites odiensis* noted above is very badly preserved, but nevertheless retains traces of constrictions in the umbilical region, indicating that a further species is present in the area. It is specifically indeterminate.

Occurrence. Cenomanian III, Zululand.

Zelandites sp. 2
(Pl. 14, fig. 1)

Material. A single specimen, SAM 7100 from the late Santonian to early Campanian Umzamba Formation at Loc. 1, the mouth of the Umzamba River, southern Natal (Pondoland).

Discussion and Occurrence. M. R. Cooper of the South African Museum has kindly sent us photographs (Pl. 14, figs 1a–b) of a further *Zelandites*, from the Umzamba Formation. The whorl section and coiling recall *Zelandites varuna* (Forbes) although constrictions appear to be absent.

Genus *KOSSMATELLA* Jacob, 1907

Subgenus *KOSSMATELLA* Jacob, 1907

Type species. *Ammonites agassizianus* Pictet 1848, by original designation.

Diagnosis. The coiling is moderately involute, the whorl section depressed to compressed. The flanks bear deep constrictions, between which are radial folds varying from mere swellings to massive protruberances. The surface of the test is finely lirate.

Discussion. Two subgenera are recognized in *Kossmatella*, *K.* (*Kossmatella*) and *K.* (*Guderianites*) Wiedmann, 1962, with *Kossmatella costata* Douvillé (1916) as type species. *Guderianites* is typified by the invariable presence of more than one swelling between constrictions. The subgenus *K.* (*Murphyella*) Matsumoto, 1972 (type species *K.* (*M.*) *enigma* Matsumoto, Muramoto & Takahashi, 1972 : 210; pl. 33, figs 1–3; text-fig. 1) is regarded as a synonym of *Anagaudryceras* Shimizu 1934.

Wiedmann (1962*a*, *b*) and Wiedmann & Dieni (1968) provide an extensive review of the genus and subgenus, and the following arrangement has been proposed on the basis of ornamentation.

1. The group of *Kossmatella agassiziana*, with radial folds, sometimes weakly bullate, including: *K. agassiziana* (Pictet) (Wiedmann 1962*a* : pl. 13, figs 9–11), Middle to Upper Albian of southern Europe. *K. romana* Wiedmann (1962*a* : 164; pl. 8, figs 6–7; pl. 13, fig. 12; text-figs 21–24), Middle and Upper Albian of southern France, the Balearics, northern and south-eastern Spain, and possibly South Africa (Zululand). *K. jacobi jacobi* Wiedmann (1962*a* : 167, *nom. nov.* for *K. agassiziana* var. II of Jacob 1908 : pl. 2, fig. 4), and *K. jacobi quenstedti* Wiedmann (1962*b* : 59; pl. 5, fig. 5; text-fig. 20), both Lower Albian of southern France and the Balearics. *K. marut* (Stoliczka 1865 : 162; pl. 17, figs 3–3c), Upper Albian of southern India and South Africa (Zululand), and the Middle Cenomanian (?) of Madagascar. *K. sublaevis sublaevis* Wiedmann (1962*b* : 52; pl. 4, fig. 7; text-fig. 17), *K. sublaevis pachys* Wiedmann, 1962*b* : 54; pl. 4, figs 2, 8; text-fig. 18) and *K. sublaevis involuta* Wiedmann (1962*b* : 56), all Lower to Upper Albian of southern France, the Balearics, Sardinia and Zacatecas (Mexico). *K. muhlenbecki* (Fallot 1885 : 233; pl. 4, fig. 1), Upper Albian of southern France, northern Spain and Sardinia.
2. The group of *Kossmatella ventrocincta*, with strong umbilical nodes, including: *K. ventrocincta* (Quenstedt 1847–8 : 223; pl. 17, figs 14a–b) and *K. ventrocincta gignouxi* Breistroffer (1931 : 193), both Middle Albian of southern France. *K. oosteri oosteri* Breistroffer (1936*a* : 1492) and *K. oosteri passendorferi* Wiedmann & Dieni (1968 : 41), Upper Albian of Switzerland, southern France, Sardinia and Poland. *K. schindewolfi* Wiedmann & Dieni (1968 : 41; pl. 3, fig. 13; pl. 4, figs 1–3; text-figs 11–12), Upper Albian of southern France, Sardinia and Poland.

All our Zululand specimens belong to *Kossmatella* (*Kossmatella*), and to the *agassiziana* group.

Occurrence. *K.* (*Kossmatella*) ranges from the ? Upper Aptian to Lower and ? Middle Cenomanian. Its chief occurrences are in the western Mediterranean region, the distribution covering southern France, Spain, the Balearics, Sardinia, Italy, Poland, north Africa, southern India, Madagascar, South Africa (Zululand), Mexico, California and Alaska. *K.* (*Guderianites*) occurs in the Albian of Sinai and possibly the Lower Albian of the Balearics.

Kossmatella* (*Kossmatella*) *marut (Stoliczka)
(Pl. 14, fig. 8)

1865 *Ammonites marut* Stoliczka : 162; pl. 79, figs 1–1b.
1895 *Lytoceras* (*Gaudryceras*) *marut* (Stoliczka) Kossmat : 130; pl. 17, figs 3–3c.
1956 *Kossmatella marut* (Stoliczka) Collignon : 66.
1963 *Kossmatella* aff. *marut* (Stoliczka); Collignon : 20; pl. 249, fig. 1065.

HOLOTYPE. By monotypy, Stoliczka's original specimen (1865 : pl. 79, figs 1–1b) from the Upper Albian of Odium, southern India.

MATERIAL. One specimen, BM(NH) C78762 from Bed 12 of the Mzinene Formation at Loc. 51 on the Mzinene River, Zululand (Albian V).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*	*Folds*
Holotype (after Stoliczka)	14·0	4·8 (35)	5·5 (39)	0·88	6·3 (45)	17
Kossmat 1895 : 130	19·5	6·0 (31)	6·5 (33)	0·92	8·0 (41)	17
BM(NH) C78762	31·1	9·8 (32)	11·2 (36)	0·88	11·1 (36)	17/18
	23·5	8·0 (34)	8·6 (37)	0·93	9·0 (38)	–

DESCRIPTION. The coiling is moderately involute, about 50% of the previous whorl being covered. The umbilicus is of moderate size (36–38% of diameter) with a low, sloping, rounded wall, which merges imperceptibly with the flanks. The whorl section is compressed, the greatest breadth being some way below mid-flank. The flanks are gently rounded and merge, via broad, gently rounded shoulders, into an evenly rounded venter.

Ornament consists of broad, band-like radial lateral folds separated by narrower constrictions; there are seventeen folds on the outer whorl. These arise as broad swellings at the umbilical seam, and pass straight across the flanks, broadening and weakening as they do so, and eventually merging with the flanks at the ventrolateral shoulder.

The constrictions are narrow and rectiradiate. Most are clearly visible only on the flanks, but some continue over the venter to form a distinct peaked constriction over the siphonal area.

The test surface of the available specimen is corroded, and no trace of lirae remains. The sutures are not visible.

DISCUSSION. Our specimen clearly matches Stoliczka's small holotype and the rather larger specimen figured by Kossmat, apart from minor differences in relative proportions. When compared with other members of the *agassiziana* group, differences are clear, if subtle; given larger populations a reduction of the large number of species names currently in use may be possible. Comparisons are as follows.

Kossmatella agassiziana itself (Wiedmann 1962*a* : pl. 13, figs 9–11) has rather similar relative proportions, but has fewer (12) and narrower lateral folds, which flex backwards on the flanks. *K. romana* Widemann (1962*a* : 164; pl. 8, figs 6, 7; pl. 3, fig. 12; text-figs 21–24; 1962*b* : 50; pl. 3, fig. 8; pl. 4, figs 1, 5; pl. 5, fig. 3) is a depressed form with coarser folds and a lower expansion rate than *K. marut* – as is *K. jacobi* Wiedmann (1962*a* : 167; 1962*b* : 56, 57; pl. 4, fig. 4; text-fig. 19; 1962*b* : 59; pl. 5, fig. 5; text-fig. 20). *K. muhlenbecki* (Fallot) (Wiedmann 1962*a* : 168; pl. 8, figs 5–8; text-figs 27–29) is a depressed slowly expanding species with 15 coarse lateral bulges per whorl, and a test ornamented by very coarse lirae. *K. sublaevis sublaevis* Wiedmann, *pachys* Wiedmann and *involuta* Wiedmann (1962*b* : 52; pl. 4, figs 2, 7, 8; text-figs 17–18) are slowly expanding forms, ornamented by faint, irregular bulges separated by broad constrictions.

OCCURRENCE. Upper Albian of South Africa (Zululand) and southern India. Middle ? Cenomanian of Madagascar.

***Kossmatella (Kossmatella)* aff. *romana* Wiedmann**
(Pl. 14, figs 5, 7, 9, 10)

1962*a* *Kossmatella romana* Wiedmann: 114; pl. 8, figs 6–7; pl. 13, fig. 12; text-figs 21–24.
1962*b* *Kossmatella* (*Kossmatella*) *romana* Wiedmann: 50; pl. 3, fig. 8; pl. 4, figs 1, 5; pl. 5, fig. 3.
1968 *Kossmatella* (*Kossmatella*) *romana* Wiedmann: Wiedmann & Dieni: 38; pl. 1, figs 10, 11; pl. 2, fig. 7; pl. 3, fig. 10.

MATERIAL. Four specimens, SAS Z539a–b and BM(NH) C78763–4 from the Mzinene Formation at Loc. 56 on the Mzinene River, Zululand (Albian V).

DIMENSIONS.	*D*	*Wb*	*Wh*	*Wb/Wh*	*U*
BM(NH) C78763	27·8	9·5 (34)	9·4 (34)	1·01	10·8 (39)
BM(NH) C78764	35·0	12·0 (34)	12·0 (34)	1·0	13·5 (38·5)
SAS Z539a	27·0	9·5 (35)	9·7 (36)	0·98	9·7 (36)

DESCRIPTION. The coiling is evolute, about 20% of the previous whorl being covered. The whorl section varies from slightly depressed during early growth stages to slightly compressed later. The umbilicus is broad, 36–39% of diameter, and shallow. The umbilical wall is low, rounded and gently sloping; the flanks are weakly inflated, the greatest breadth being a little below mid-flank. The ventrolateral shoulder is rounded, merging into a broad, evenly rounded venter. The flanks bear 17–19 lateral bulges per whorl; these arise at the umbilical seam, are at their maximum strength on the lower flank, declining on the upper flank, and disappearing by the ventrolateral shoulder. The intervening constrictions are quite narrow, rectiradiate to slightly prorsiradiate, and distinctly peaked on the venter; up to seven of these per whorl are deeply incised on the internal mould, although all are relatively weak where shell is preserved.

The surface of the test, when preserved, is covered in fine dense lirae. The sutures are not seen.

DISCUSSION. The striking features of our specimens are the presence of strong lateral bulges, a wide umbilicus, the deep incision of occasional constrictions and the rather broad whorl section. *Kossmatella marut* is more compressed, with weaker bulges, as is *K. agassizianum*, where the lateral bulges are fewer (12 per whorl) and flexed. *K. jacobi* and its variety *quenstedti* are more inflated and more robustly ornamented. *K. muhlenbecki* has a markedly tabulate venter and other distinctive characters, whilst forms such as *K. laevis* and its varieties are even more distinctive, as noted above.

The most obvious comparisons are thus to be made with *Kossmatella romana* Wiedmann. The published figures show a range of variability in specimens referred to the species; in general, specimens retaining their test have somewhat stronger lirae and coarser lateral bulges than our specimens, whilst internal moulds lack the occasional deeply-incised constrictions of our material. The Zululand specimens may represent a new species, or a subspecies of *K. romana*, but we would hesitate to introduce a new name on the basis of the present limited material.

OCCURRENCE. *Kossmatella romana* occurs in the Middle and Upper Albian of France, the Balearics, south-eastern and northern Spain, and Sardinia; our Zululand material is of Upper Albian age.

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R. Watkins

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Synopsis

Five areas of the Ludlow Series in the Welsh Borderland have been studied by quantitative, stratigraphic sampling to determine community organization on an Upper Silurian shelf. Measured sections show an ordered succession of predominantly terrigenous facies, with an environmental gradient of general shallowing, increasing grain size, decreasing clay content, decreasing bioturbation, and increase in storm-deposited beds of laminated silt and shells. This sequence is interrupted by low energy, back-barrier carbonates in the Upper Bringewood Beds. Shell transport occurred commonly during deposition of proximal shelf silts, and was related to a storm-generated, suspension type of movement which did not contribute to shell breakage or abrasion. Sorting of epifaunal brachiopods into concentrated layers is the most significant, taphonomic effect of transport.

Stratigraphic profiles of fauna, based on continuous series of samples at 1 m vertical intervals, are used to define six communities in measured sections, dominated by articulate brachiopods, bryozoa, molluscs and trilobites. Substrate sedimentation processes and hydrographical history of the depositional area were important factors influencing Ludlow shelf faunas, and an overall control by the physical environment appears to have shaped community organization. Decline in species diversity, increase in opportunistic species and changes in faunal composition occur along the distal to proximal shelf gradient in

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stratigraphic sections. These changes correlate with increased rates of sedimentation and frequency of storm-sedimentation events. Trophic structures in Ludlow shelf communities appear to have been relatively simple, dominated by low level suspension feeding and deposit feeding at the same sites. Encrustation of shells and rare predatory borings are the only preserved evidence of biotic interaction.

During intervals of environmental constancy, stratigraphic variation occurs within communities, but results in no biologically controlled or directional trends. In proximal shelf environments, intracommunity variation is extreme and unpredictable, but in distal shelf environments, predictable cycles in abundance of particular species occur in vertical intervals of several metres. Intracommunity variation in distal shelf environments does not conform to models of ecological succession, is not accompanied by any sedimentary changes, and is not affected by benthic faunal destructions represented by bentonites. A model of pelagic environmental effects upon larval recruitment is the best explanation for the phenomenon.

Number and discreteness of Ludlow shelf communities, as well as diversity, population strategies and faunal composition were primarily controlled by the physical environment, and the major faunal patterns in stratigraphic sections are products of the environmental history of the depositional area. Variation within particular communities and within particular habitats is superimposed upon these patterns, and is probably related mainly to pelagic effects upon larvae, with a large random component. A consequence of this simple, physically-controlled community structure is quantitative stability of composition and diversity in terrigenous shelf communities from at least early Silurian until early Devonian times. There is no evidence for 'biological accommodation', or progressive niche-partitioning, in Silurian communities of stable, distal shelf environments.

Introduction

This study is a quantitative, stratigraphic analysis of community organization in marine bottom faunas in the Ludlow Series of the Welsh Borderland. The Ludlow of this area is a sequence of dominately terrigenous strata deposited under open marine, shelf conditions. It is the uppermost division of Murchison's original Silurian System, and has been intensively studied by palaeontologists and stratigraphers for the past 140 years. Lawson (1975) has reviewed earlier work, and given an important preliminary account of ecological divisions in the Ludlow fauna.

In contrast to previous studies of Silurian palaeoecology in the Welsh Borderland, such as Hancock, Hurst & Fürsich (1974), the environmental analysis in this report is established independently of faunal data. Sedimentological study of selected measured sections has been used to establish physical, environmental gradients. The vertical sequence of Ludlow terrigenous sediments is considered as a cross-section from distal to proximal shelf depositional environments (Walther 1894 : 979). Physical sedimentary effects were far more important in determining community patterns in Silurian shelf faunas than previous studies would indicate.

Stratigraphic patterns of fauna in Ludlow sections have been described with closely spaced quantitative samples. Detailed faunal data have been derived from this sampling, and these data are related to the sedimentary-environmental gradients observed in sections. The work is not intended to provide complete areal coverage of the Welsh Borderland, or define any standard bathymetric sequence of Ludlow communities; instead, its primary purpose is a consideration of biological and environmental aspects of community organization in selected measured sections of shelf sediments.

Stratigraphic patterns in fauna within measured sections show both between and within habitat components, involving directional trends along environmental gradients and non-directional fluctuations. As a matter of convenience, these patterns are described as six named 'Associations' of species. In the concluding parts of this report, the faunal and environmental data are compared with models of ecological organization, which consider aspects of biotic interaction, environmental response and ecological succession in marine communities. This comparison establishes some of the important biological and environmental aspects of Ludlow community organization in the Welsh Borderland, and has general applicability to Silurian shelf faunas.

Methods

Stratigraphic sections

Fig. 1 shows the five areas in the Welsh Borderland where stratigraphic sections were measured.

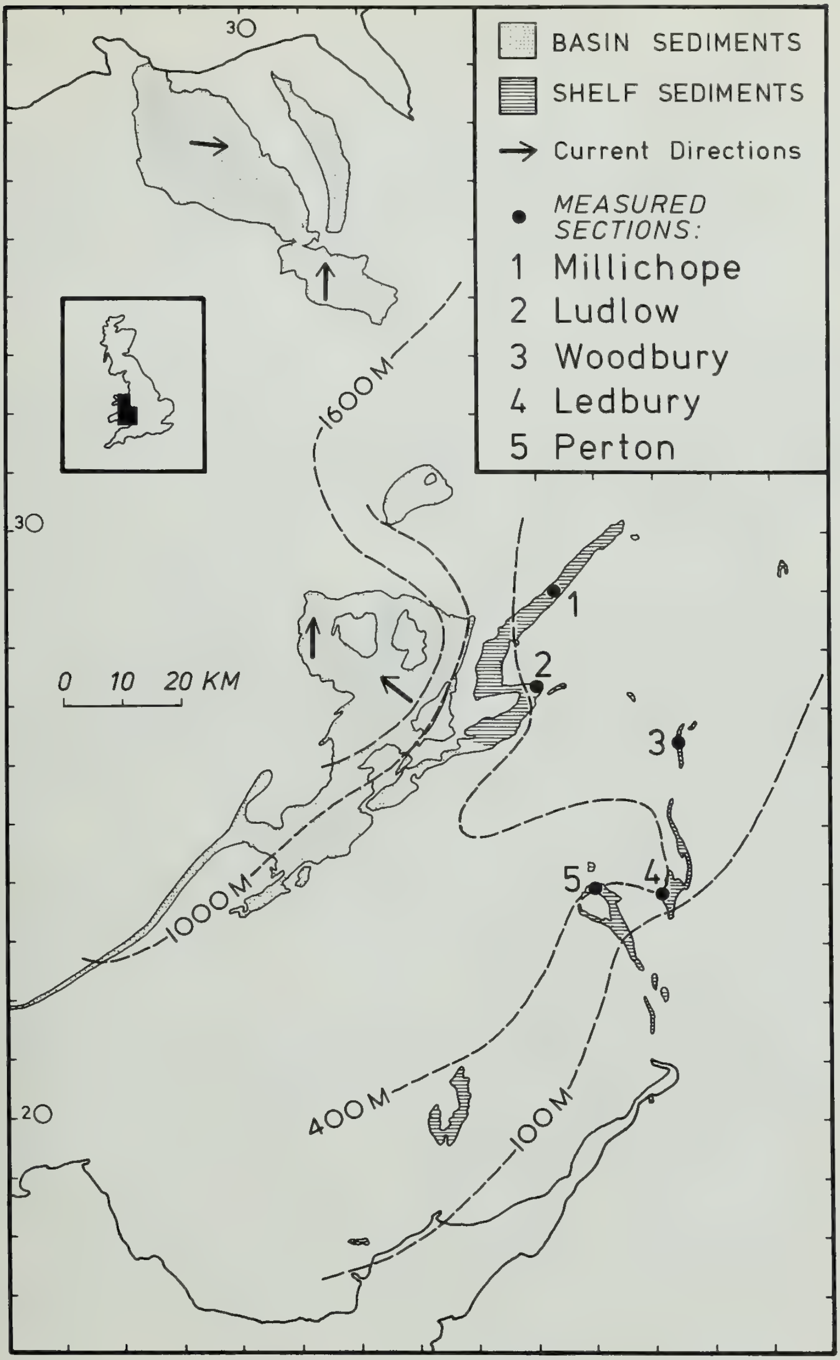

BASIN SEDIMENTS
SHELF SEDIMENTS
Current Directions
MEASURED SECTIONS:
1 Millichope
2 Ludlow
3 Woodbury
4 Ledbury
5 Perton
30
30
20
0 10 20 KM
1600M
1000M
400M
100M
1
2
3
4
5

Fig. 1 Ludlow outcrop of Wales and the Welsh Borderland, showing the location of study areas. Isopachytes and current directions are adapted from Holland & Lawson (1963).

These areas were selected to obtain detailed coverage of a particular part of the Ludlow shelf deposits, and do not record the full complexity of Ludlow faunas and sediments in the Welsh Basin. Because of limited outcrop in most areas, many small, isolated sections had to be measured to obtain a composite record of the succession. The 27 separate sections are shown in Fig. 2, and their locations are described in Appendix 1, p. 258).

Sections were measured directly with tape, and the sequence and thickness of all sedimentation units recorded to the nearest cm. The principal sedimentation units recorded were bioturbated sediment, simple laminated beds, amalgamated laminated beds, bentonites and shell beds or layers. Textures were qualitatively noted in the field, and checked in the laboratory with thin sections of representative samples. Over 100 saw-cut slabs were prepared for observation of sedimentary structures.

Sampling of fauna

The purpose of palaeontological sampling was to produce a quantitative faunal profile of each stratigraphic section, based on numerous equally-spaced sampling points. Bulk rock was collected, and not individual fossils. In each section, the samples of bulk rock were taken at distances as near as possible to 1 m apart stratigraphically. Closer sample spacing was used in a few sections to study small-scale ecological phenomena, and wider spacing was necessary where rock could not be removed from sheer faces of large quarries. The 1 m spacing distance governed the location of samples, and not the presence of abundant or well-preserved fossils. This practice was modified, however, in the lowest Lower Leintwardine Beds of Woodbury and Perton Quarries, where fossils are very rare except in transported shell layers.

The stratigraphic thicknesses of bulk rock samples are given in Appendix 3, p. 268. These ranged generally from 1 to 20 cm, and most samples were about 4000 cm^3 in volume. No attempt was made to standardize sample volumes, however, and density was not the basis for palaeontological quantification. Most samples were taken from a single sedimentation unit.

The samples of bulk rock were split along fissile surfaces parallel to bedding, and all observed macrofossils were counted. One hundred and twenty-two samples were prepared in the field with hammer and chisel. These samples were restricted to low-diversity faunas of the Whitcliffe Beds, Leintwardine Beds and Upper Bringewood Beds, and were made only after eight months of laboratory work on similar samples, in which a thorough familiarity with species was obtained. The remaining 295 samples were processed in the laboratory with a mechanical rock splitter. Most fossils were decalcified with dilute hydrochloric acid to obtain internal and external moulds.

Palaeontological quantification

Because of the variation in sedimentary facies and probable rates of deposition in Ludlow shelf deposits, volumetric densities of fossils are not reliable for sample comparisons. In this study the basis for standardizing and comparing the faunal content between samples is relative abundance. Relative abundances were calculated within each sample for each taxonomic category under consideration (usually species). The relative abundance of a taxon is defined as the number of individuals of the taxon divided by the total number of individuals within the sample, expressed as a percentage. These percentages are plotted along stratigraphic columns in the sections on community definition, pp. 213–221, and form the primary basis for community analysis.

Arbitrary criteria were defined for recording over 33 000 'individuals' from the measured sections. The purpose of these criteria was consistency in quantification of samples, and not an absolute determination of the biological equivalence of different groups. Individuals were counted directly for gastropods, tentaculitids, cornulitids, annelids, hyolithids and solitary corals. Individuals were arbitrarily defined for other groups, as follows.

Brachiopods: number of individuals of a species = articulated shells + maximum number of either pedicle or brachial valves + half the number of indeterminate single valves.

Bivalves: individuals counted as for brachiopods, except that maximum number of either right or left valves was used.

Cephalopods: These fossils are preserved as phragmocones, body chambers, fragments of either, or isolated cameral and septal moulds. All pieces were scored as 1 individual, and as 2 or fewer specimens were encountered in most samples, this did not greatly exaggerate their abundance.

Trilobites: The individuals per species in each sample were counted as the number of pygidia present, or if no pygidia but other elements were present, as 1 individual. Trilobites are sufficiently rare for this method not to exaggerate their abundance in most samples.

Bryozoa: Number of individuals were defined as the number of separate bryozoan pieces observed macroscopically in each sample. No attempt was made to distinguish separate species within this phylum. Globular and encrusting bryozoa are usually preserved intact, so that 'individuals' are direct counts of colonies. Ramose forms are usually fragmented, and the number of individuals counted is partly an effect of the degree of fragmentation.

Tabulates: Number of individuals was counted as number of colonies within a sample.

Variable numbers of individuals were obtained in each sample, as indicated in Appendix 3. A detailed evaluation of the reliability of sampling, based on the number of individuals per sample, is given in Appendix 2, p. 260.

Diversity was measured within each faunal sample as the number of species obtained at a sample size of 50 individuals. This measurement was made by direct count of species in samples containing 50 individuals, and by application of the rarefaction method of Sanders (1968) to samples of larger size.

Deposition of data and collections

Only a limited amount of quantitative faunal data is presented here; full data have been deposited in the Palaeontology Library of the British Museum (Natural History), Cromwell Road, London SW7 5BD, as discussed in Appendix 3. The collections of brachiopods, cephalopods and encrinurid trilobites, representing about 85% of total collections, have also been deposited in the Department of Palaeontology, British Museum (Natural History); specimens of other groups are deposited in the University of California Museum of Paleontology, Berkeley, Calif., U.S.A.

Stratigraphy

Stratigraphic classification of the measured sections

The stratigraphic units represented by measured sections are shown in Fig. 2, using the classification of Holland, Lawson & Walmsley (1963). Working in the type area around the town of Ludlow, these authors defined nine stratigraphic divisions, termed 'Beds,' within the Ludlow Series. They stated (1963 : 114) that 'the divisions have been mapped mainly on the basis of their faunal assemblages but lithological characteristics have also proved very helpful in their identification.' In the present study, faunal criteria have been used to recognize the divisions outside of their type sections, and the pertinent data are contained in stratigraphic profiles of fauna presented in the community definition section, p. 208, as well as Appendix 3. These criteria followed the descriptive characteristics of the divisions given by Holland *et al.* (1963), with the exceptions noted below.

The basal division of the Ludlow Series, the Lower Elton Beds, is not considered in this study. A recent account of its stratigraphical palaeoecology has been given by Hurst (1975*a*).

Recognition of the Lower and Upper Bringewood Beds

The stratigraphical position of the Bringewood Beds in the Ludlow succession is shown in Fig. 2. Although most authors have recognized a division into Lower and Upper Bringewood Beds throughout the Welsh Borderland, there has been little consistency of usage east of the type area at Ludlow. This section will define the way these stratigraphic divisions are recognized here.

Within the type area near Ludlow, Holland *et al.* (1963) defined the Upper Bringewood Beds as a silty limestone gradationally overlying calcareous siltstone of the Lower Bringewood Beds.

These authors gave full faunal lists for each division; the fauna of the Lower Bringewood Beds corresponds to the *Mesopholidostrophia laevigata* Association of this report. The Upper Bringewood Beds in the type area also contain the *M. laevigata* Association, and are faunally distinguished from the Lower Bringewood Beds by the presence of *Kirkidium knightii* and large tabulate corals (Holland *et al.* 1963). This same faunal distinction applies to the Leintwardine and Aymestrey areas west of Ludlow, the main difference being that *Kirkidium* and corals locally constitute most of the fauna of the Upper Bringewood Beds (Whitaker 1962; Lawson 1973*a*).

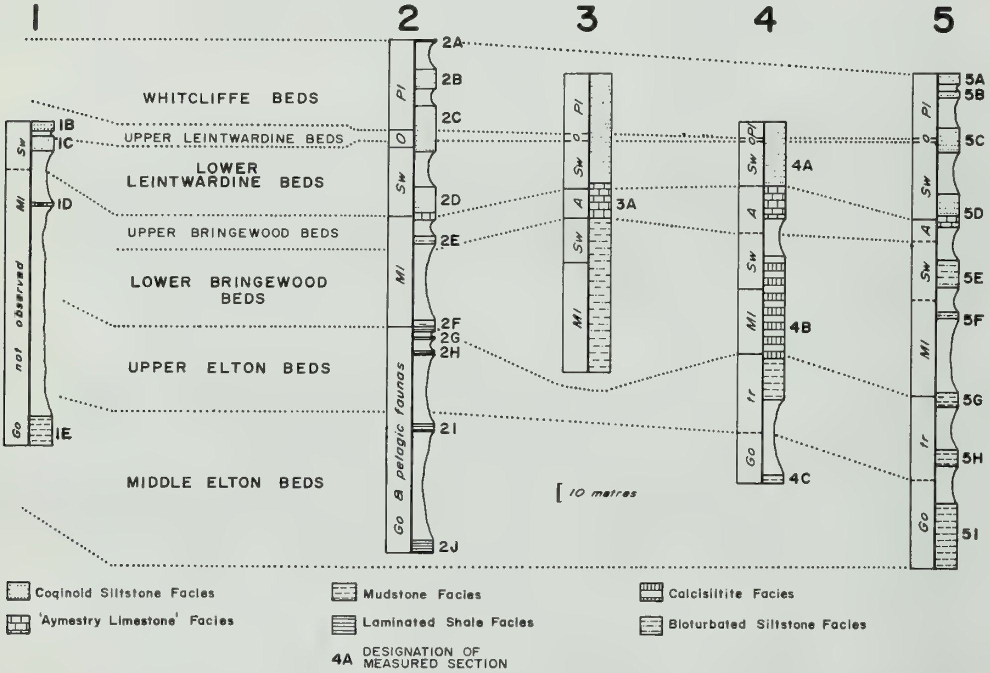

1
2
3
4
5
WHITCLIFFE BEDS
UPPER LEINTWARDINE BEDS
LOWER LEINTWARDINE BEDS
UPPER BRINGEWOOD BEDS
LOWER BRINGEWOOD BEDS
UPPER ELTON BEDS
MIDDLE ELTON BEDS
1B
1C
1D
1E
Sw
Ml
not observed
Go
2A
2B
2C
2D
2E
2F
2G
2H
2I
2J
Pl
O
Sw
Ml
Go & pelagic faunas
3A
Pl
O
Sw
A
Sw
Ml
4A
4B
4C
Sw
O
Pl
A
Sw
Ml
tr
Go
5A
5B
5C
5D
5E
5F
5G
5H
5I
Pl
O
Sw
A
Sw
Ml
tr
Go
10 metres
Coqinoid Siltstone Facies
'Aymestry Limestone' Facies
Mudstone Facies
Laminated Shale Facies
Calcisiltite Facies
Bioturbated Siltstone Facies
4A DESIGNATION OF MEASURED SECTION

Fig. 2 Stratigraphic summary of the measured sections. Numbers refer to map locations in Fig. 1; detailed locality descriptions of each section are given in Appendix 1, p. 258. A complete sequence of all Ludlow stratigraphic units is present in every area, but only those intervals which were observed are shown. The left portion of each column indicates benthic communities as follows: *Pl – Protochonetes ludloviensis* Association; *O – Shaleria ornatella* Assoc.; *Sw – Sphaerirhynchia wilsoni* Assoc.; *A – Atrypa reticularis* – coral Assoc.; *Ml – Mesopholidostrophia laevigata* Assoc.; *tr* – transitional fauna; *Go – Glassia obovata* Assoc.

These relations are compared in Table 1 to the succession of Bringewood faunas east of Ludlow. At Woodbury Quarry and in the Perton area (Fig. 1), the *M. laevigata* Association is overlain by the lower phase of the *Sphaerirhynchia wilsoni* Association, which is in turn succeeded by the *Atrypa reticularis* – coral Association. The two lower faunas occur in calcareous siltstone, and the upper fauna in silty limestone, although both lithologies are highly gradational. Graphic charts of the species ranges which define these associations are given in Figs 17 (pp. 214–5) and 20 (p. 218), and full faunal lists are given in Appendix 3. For the purpose of this report, the Lower Bringewood Beds in these areas are defined as the *M. laevigata* Association and lower phase of the *S. wilsoni* Association, and the Upper Bringewood Beds are defined as the *Atrypa reticularis* – coral Association.

This usage differs from that of previous workers in the Woodbury and Perton areas. In the Perton Lane section, Squirrell & Tucker (1960) drew a boundary between their Lower Sleaves Oak Beds and Upper Sleaves Oak Beds at an interval which falls in the middle of section 5E of the present report (Fig. 2). This boundary was later redefined, with the Sleaves Oak Beds as the boundary between the Lower Bringewood Beds and Upper Bringewood Beds (Curtis *et al.* 1967). It falls within the lower phase of the *Sphaerirhynchia wilsoni* Association and does not correspond to the boundary of Lower and Upper Bringewood Beds recognized here.

Table 1 The definition of Lower and Upper Bringewood Beds followed in this report. The distinction of these units in the Woodbury Quarry, Ledbury and Perton areas differs from that of previous authors. In section 4B near Ledbury, Penn *et al.* (1971) placed the boundary of Leintwardine and Bringewood Beds between faunas here called the lower phase of the *S. wilsoni* Association and the *M. laevigata* Association. At Perton, Curtis *et al.* (1967) placed the boundary of Lower and Upper Bringewood Beds within the lower phase of the *S. wilsoni* Association in section 5E

	Leintwardine and Aymestrey areas	Ludlow area (type sections)	Woodbury Quarry, Ledbury and Perton areas
Lower Leintwardine Beds	upper phase of *Sphaerirhynchia wilsoni* Association	upper phase of *Sphaerirhynchia wilsoni* Association	upper phase of *Sphaerirhynchia wilsoni* Association
Upper Bringewood Beds	locally abundant *Kirkidium knightii* and tabulate corals	*Mesopholidostophia laevigata* Association with few *Kirkidium knightii* and tabulates	*Atrypa reticularis* – coral Association
Lower Bringewood Beds	*Mesopholidostrophia laevigata* Association	*Mesopholidostrophia laevigata* Association	lower phase of *Sphaerirhynchia wilsoni* Association *Mesopholidostrophia laevigata* Association

Two areas of Bringewood Beds were studied near Ledbury, section 4A, at the north end of Frith Wood, and section 4B, near Knapp Lane (see detailed locations in Appendix 1). The intervening area is poorly exposed and structurally complex (Phipps & Reeve 1969), and superpositional relations of the sections have been established on faunal grounds (Fig. 2). In section 4A, the Bringewood Beds consist of silty, nodular limestone containing the *A. reticularis* – coral Association. These strata are assigned to the Upper Bringewood Beds, and are overlain by the Lower Leintwardine Beds.

In section 4B, the Bringewood Beds consist of silty and argillaceous limestones bearing the *M. laevigata* Association in their lower portion, and the lower phase of the *S. wilsoni* Association at their top. Both faunas are assigned to the Lower Bringewood Beds, and a detailed profile of the section is shown in Fig. 19, p. 217. However, Penn *et al.* (1971 : 19) assigned strata at the top of this section, bearing the *S. wilsoni* Association, to the 'basal Leintwardine Beds'. Although ecologically similar to the fauna of the Lower Leintwardine Beds, the fauna at the top of section 4B includes *Dalejina hybrida*, *Strophonella euglypha*, *Mesopholidostrophia laevigata*, *Gypidula lata*, *Eospirifer radiatus* and *Dalmanites myops*, which are more characteristic of the Bringewood Beds.

Synchrony of Ludlow stratigraphic divisions

Holland *et al.* (1963) and most subsequent authors have considered their nine stratigraphic divisions as valid units of time for Ludlow shelf deposits of the Welsh Borderland. Lawson (1975) has noted that while most of the stratigraphic ranges of Ludlow benthic invertebrates are under facies control, the synchrony of the stratigraphic divisions is supported by graptolite evidence.

These conclusions are also upheld by the ecological analysis presented in this report. Following the concept of 'causal biostratigraphy' (Krassilof 1974), two community phenomena in Ludlow shelf sections can be explained ecologically only if they are considered synchronous. The first of these is the Upper Bringewood fauna, in which the restricted *Atrypa reticularis* – coral Association appears as a stratigraphic anomaly in inner shelf sections. This fauna can be accounted for as having occupied some sort of restrictive, back-barrier environment. There is only one interval in sections at the shelf edge area which includes barrier-type deposits, and this is the Upper Bringewood Beds containing 'banks' of *Kirkidium* and large corals. Synchrony of the Upper Bringewood Beds between these areas (as redefined in this report) is therefore highly likely.

The second synchronous ecologic phenomenon is the appearance of the distinctive fauna of the Upper Leintwardine Beds, which occupies only 1–5 m of strata in the Welsh Borderland, but occurs across the whole of the shelf area (Lawson & Straw 1956; Holland *et al.* 1963). This appearance involves the very short-lived colonization of proximal shelf deposits by forms from quiet-water, distal shelf communities. It can be explained ecologically only by brief, synchronous changes in shelf-wide current patterns controlling larval dispersal.

Both of these ecological phenomena and their causal explanations are discussed more fully on pp. 231–237. The stratigraphic position of the Upper Bringewood Beds and Upper Leintwardine Beds is shown in Fig. 2. The Middle Elton Beds, lower in the sequence, can be considered as synchronous across the Welsh Borderland by their content of *nilssoni* Zone and *scanicus* Zone graptolites (Holland *et al.* 1963, 1969; Shergold & Shirley 1968). From Fig. 2, it can be seen that synchrony of these three units effectively brackets the Ludlow shelf sequence, indicating a synchrony for each of the units between.

Sedimentology

Distinction of Ludlow basin and shelf

The Ludlow sediments of Wales and the Welsh Borderland form two environmental complexes, a basin facies to the west, and a shelf facies to the east (Fig. 1). Basin deposits range from 500 to

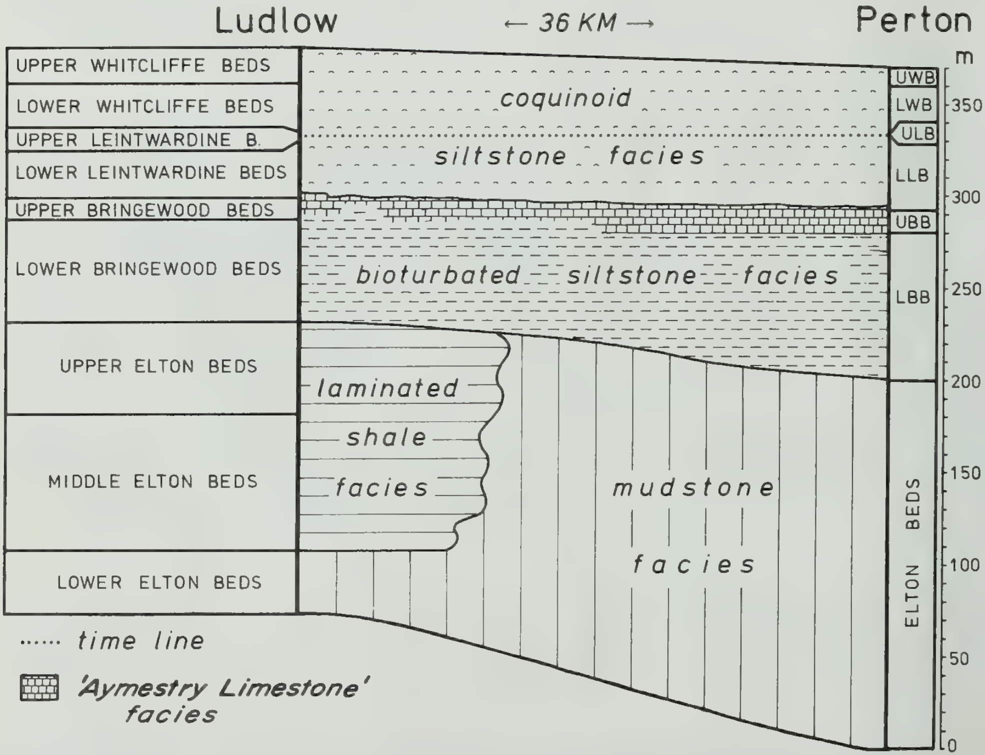

Ludlow
← 36 KM →
Perton
m
UPPER WHITCLIFFE BEDS
LOWER WHITCLIFFE BEDS
UPPER LEINTWARDINE B.
LOWER LEINTWARDINE BEDS
UPPER BRINGEWOOD BEDS
LOWER BRINGEWOOD BEDS
UPPER ELTON BEDS
MIDDLE ELTON BEDS
LOWER ELTON BEDS
coquinoid
siltstone facies
bioturbated siltstone facies
laminated shale facies
mudstone facies
UWB
LWB
ULB
LLB
UBB
LBB
ELTON BEDS
350
300
250
200
150
100
50
0
time line
'Aymestry Limestone' facies

Fig. 3 Generalized cross-section showing stratigraphic relationships of the sedimentary facies described in the text.

over 1600 m thick (Holland & Lawson 1963). They consist of laminated siltstone and mudstone, siltstone and shelly turbidites, and common slumped masses of beds (Cummins 1959, 1969; Bailey 1964, 1969). The basin–shelf margin lay along the line of the Church Stretton fault, as indicated by rapid increase in sedimentary thickness to the west and westward orientation of slump directions (Holland & Lawson 1963; Bailey 1969). Cummins (1959) showed a direction of turbidite transport from the south in central Wales and from the south and west in north Wales (Fig. 1). Graptolites are most diverse throughout the Ludlow Series in Clwyd or north central Wales, indicating open-ocean connections along the north of the basin (Wood 1900; Warren 1971; Holland & Palmer 1974).

The bordering Ludlow shelf deposits are less than 500 m thick, and thin out towards the south-east (Fig. 1). They consist of bioturbated calcareous siltstone and mudstone, and include minor limestone. Depositional facies are described below for the five study areas, and are shown as a cross-section in Fig. 3. The stratigraphic sections measured within each facies are indicated in Fig. 2. This section is not an attempt to chart the complete history of Ludlow sedimentation in the Welsh Borderland, which is beset with numerous (and interesting) complexities in areas beyond the measured sections. Such a historical approach has been given by Holland & Lawson (1963), who provide a series of palaeogeographic maps. The present study is orientated toward sedimentology of vertical sections, and establishes environmental gradients used in the following palaeoecological analysis.

Petrography and diagenesis of Ludlow shelf sediments

Terrigenous sediments encountered range from equal mixtures of clay and silt to fine sandy siltstone, with quartz and mica as the predominant grains. Feldspar and other minerals comprise

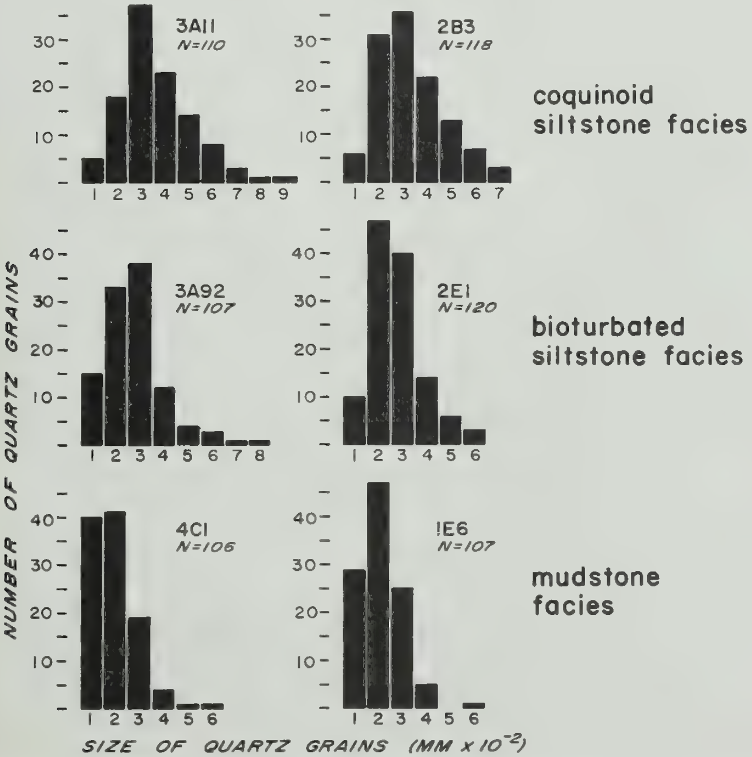


Fig. 4 Size distribution of detrital quartz grains, based on direct measurement to 0·01 mm of apparent grain diameters in thin section.

less than 2% of detrital grains. Quartz grains show low sphericity and moderate to high angularity; grain size measurements are given in Fig. 4. Clay content varies between sedimentary facies, as does the mean size of silt and sand grains. Carbonate content ranges from 7% in the finest-grained terrigenous sediments to nearly 30% in the coarsest siltstones (Holland *et al.* 1963 : 187), with marked small-scale vertical and lateral variation. Several factors suggest that much of the variation in carbonate is diagenetic – finely crystalline calcite often shows growth into detrital quartz, nodules and shell beds, discussed below, indicate diagenetic movement of carbonate, and no consistent faunal changes occur between adjacent siltstones of highly different carbonate content.

Microsparite nodules are present in all sedimentary facies. They have discrete boundaries, ellipsoidal shapes and long axes of less than 15 cm. One thin section from the Upper Elton Beds (sample 4B29) consists of 95% microsparite, 2% quartz grains, <1% mica, <1% bioclasts and 2% other material. Nodules preserve fossils three-dimensionally, in contrast to their crushed state in siltstones. In laminated beds, laminae are compressed beneath nodules and arched over their tops. Whitaker (1962) made similar observations. These features indicate post-depositional but pre-compactional formation of nodules, and attest very early diagenetic movement of carbonate.

Beds of concentrated shell material, interpreted later as high-energy storm deposits, were described by Holland *et al.* (1963) as 'shelly limestones'. These beds are usually 2–5 cm thick, and consist mainly of bioclasts and calcite cement (Table 2). In thin section, large calcite crystals are bounded by bioclasts, and completely enclose detrital grains of quartz and mica. Quartz grains show finely etched boundaries, and are sometimes intruded by small growths of calcite. Large calcite crystals completely enclosing quartz grains have also been observed in physical and optical continuity with brachiopod shells. These observations suggest replacement of quartz by calcite, and derivation of the calcite matrix from surrounding shell material. Siltstones tend to show highest carbonate content immediately around shell beds, which further suggests derivation of the calcite matrix from shells. The 'limestone' nature of these shell beds will not be considered relevant to their depositional interpretation.

Table 2 Percentage composition of shell beds based on 250–400 point counts of 1 thin section per sample. ULB – Upper Leintwardine Beds; UWB – Upper Whitcliffe Beds; LLB – Lower Leintwardine Beds; LLB – Lower Bringewood Beds

sample number	1B2	2B3	5D	5E8
stratigraphic unit	ULB	UWB	LLB	LBB
calcite cement	65	65	80	80
bioclasts	19	12	14	13
detrital quartz	6	20	5	2
detrital mica	8	3	1	3
other	2	1	1	2

Bedding

All Ludlow shelf sediments occur as tabular layers parallel to the general stratification. In the predominant bioturbated sediments, the boundaries of most layers are irregular and laterally impersistent, do not correspond to any internal sedimentary structures, and separate sediment of identical type. In Woodbury Quarry, the thick-layered strata of freshly exposed surfaces are seen to pass laterally into apparently thin-layered beds of the more weathered exposures. This type of layering, which Holland & Lawson (1963) and many others have erroneously described as 'bedding', is thus primarily a weathering feature. Primary bedding, where layers correspond to sedimentation units, is common only in the laminated shale facies of the Elton Beds and coquinoid siltstone facies of the Leintwardine Beds and Whitcliffe Beds.

Bentonites

Thin beds of clay are present throughout the Ludlow shelf facies. They are characterized by their softness, lack of fossils and sharp, parallel-sided contacts. These beds are considered as bentonites, and their thicknesses and frequency of occurrence are given in Table 3. The purest bentonites occur in the Elton Beds and Lower Bringewood Beds, where they have sharp, flat bases and appear internally homogeneous. Upper contacts are also sharp and show no burrowing, although they are overlain by thoroughly bioturbated mudstone or siltstone. Bentonites persist laterally across available outcrops.

In the Upper Bringewood Beds and Lower Leintwardine Beds, similar bentonites grade upward into silty claystone with well-developed parting planes. The silty claystones contain no fossils or bioturbation and may grade slightly into overlying sediment. They are often present without underlying, pure bentonites.

Table 3 Stratigraphic measurements of Ludlow bentonites. EB – Elton Beds; LBB – Lower Bringewood Beds; BL – Upper Bringewood and Lower Leintwardine Beds; LLB – Lower Leintwardine Beds; UWB – Upper Whitcliffe Beds; m – mudstone facies; l – laminated shale facies; b – bioturbated siltstone facies; s – calcisiltite facies; a – 'Aymestry Limestone' facies; c – coquinoid siltstone facies

section number	1E	5H, I	2I, J	1D	2D, F	3A	5E, F	4B	3A	5D	5D	5A
stratigraphic unit	EB	EB	EB	LBB	BB	LBB	LBB	LBB	BL	BL	LLB	UWB
sedimentary facies	m	m	l	b	b	b	b	s	a	a	c	c
number of bentonite beds (* incl. derived silty claystones)	3	4	8	1	2	18*	4*	3	10*	8*	9*	1*
mean bed thickness (cm)	4·3	2·8	3·4	1·0	8·5	5·3	4·5	8·3	6·6	2·6	1·8	5·0
thickness of section (m) ÷ number of bentonite beds	5·3	11·5	1·3	3·9	3·7	4·5	4·6	16·7	2·0	0·8	1·3	6·1
bentonite beds as percent of stratigraphic thickness	0·8	0·2	2·5	0·3	2·3	1·2	1·0	0·5	3·3	3·3	1·3	0·8

Mudstone facies

The mudstone facies forms most parts of the Elton Beds, and reaches thicknesses of 200 m. Sections show an extreme uniformity of texture and composition, and sedimentary structures are very rare. Clay content is about 50%, but cannot be accurately measured because of diagenesis in small mica grains. Quartz grains have an average size of about 0·02 mm, and rarely exceed 0·07 mm (Fig. 4). Shell content is generally 1–2%.

In polished section, sediments show an intricate mottling of clay-rich, dark-coloured areas and more silty, light-coloured areas (Pl. 1, fig. 5). Mottled sediment shows no discrete burrows, except for possible vertical burrow fillings of shell debris. In a few samples, mottling can be traced through intermediate stages into well-defined laminae with burrow disruptions (Pl. 1, fig. 4). Thus, the typical, mottled character of the facies results from intense deformative bioturbation.

Laminated silt beds comprise less than 1% of stratigraphic sections. They occur as isolated tabular layers 3 cm or less thick, and are continuous across outcrops of 1–2 m in extent. These beds have sharp, nearly flat erosional bases and bioturbated tops (Pl. 1, fig. 6). Parallel laminae reach thicknesses of 1 mm, and are defined by alternation of clay-rich and clay-poor silt. Maximum grain size reaches 0·2 mm, and a thin basal layer of shell debris is sometimes present. Low-angle, planar cross lamination may also occur.

A bedding type resembling the laminated shale facies occurs between 1·3 and 2 m above the base of section 5G at Perton, where beds with sharp, flat bases contain parallel lamination and grade upward into bioturbated mud and silt. They are repetitively developed at 5 cm intervals.

Laminated shale facies

The laminated shale facies reaches thicknesses of 200 m, and forms the Middle and Upper Elton Beds of the Ludlow area. Most of this sediment is identical in composition and texture to the mudstone facies, and is also very uniform in vertical profile. Bioturbation is restricted or absent through most of the facies, and the sediments have a flat, parallel lamination or well-developed parting which suggests lamination. Laminations reach 2 mm thick, and are defined by variations in clay content.

Additional sediment types occur in the Upper Elton Beds. Beds of highly calcareous, argillaceous siltstone range from 2 to 5 cm thick, with sharp, parallel, laterally continuous contacts. Graded siltstone beds also occur, reaching 2 cm in thickness with flat erosional bases. Williams & Prentice (1957) described slump structures in the Upper Elton Beds ranging from a few mm to 2 m in scale.

Bioturbated siltstone facies

The bioturbated siltstone facies is characteristic of the Lower Bringewood Beds, and forms the Upper Bringewood Beds in the Millichope area and places around Ludlow. It reaches 80 m in thickness. Except for sporadic shell beds, vertical profiles show little variation in composition and texture. Clay is present throughout, but is less abundant than silt. Quartz shows a modal grain size of 0·02–0·03 mm (Fig. 4), and may reach sizes of 0·16 mm. Shell material comprises about 1·5% of sediment volume outside of shell beds.

Most sediment shows complex mottling like that of the mudstone facies (Pl. 1, fig. 3). Traces of thin, burrow-disrupted lamination occur sporadically, and mottling is a result of intense bioturbation. *Chondrites* and small subvertical burrows are often present. Shell fragments occur in ill-defined lenticles 0·5–7 cm across which may be the result of burrowing.

Plate 1

Bioturbated Siltstone Facies

Fig. 1. Bioclastic bed within bioturbated silt, showing sharp lower contact and disturbed upper surface. Sample 5E8, Lower Bringewood Beds, Perton Lane. SO 596398.

Fig. 2. Parallel-laminated silt bed within finer-grained bioturbated silt, showing cross-sections of horizontal burrows. Near sample 3A54, Lower Bringewood Beds, Woodbury Quarry. SO 743637.

Fig. 3. Thin layer of bioclasts (interpreted in text as 'swell-lags') within bioturbated silt. Sample 3A57, Lower Bringewood Beds, Woodbury Quarry. SO 743637.

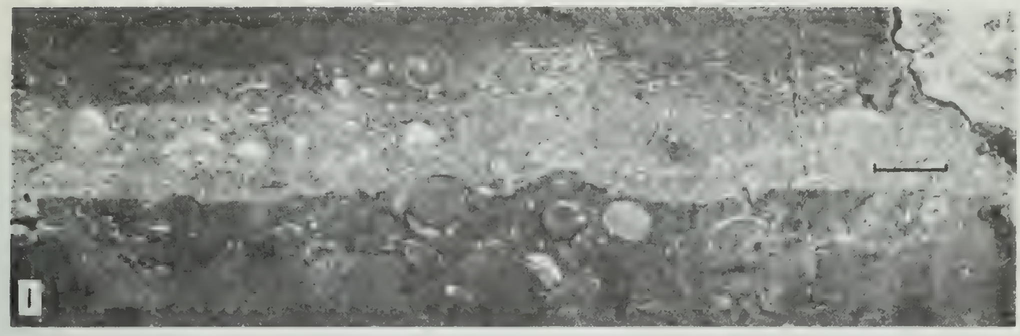
Mudstone Facies

Fig. 4. Interbedded laminated silt and mud showing the effects of intense bioturbation. This sample is from a transitional interval between the Mudstone Facies and Bioturbated Siltstone Facies. Sample 5G6, Upper Elton Beds near Perton. SO 592395.

Fig. 5. Typical appearance of the Mudstone Facies, showing mottling produced by intense deformative bioturbation and scattered, variably orientated shell material. Sample 4C1, Middle Elton Beds near Ledbury. SO 715386.

Fig. 6. Upper portion of a rare laminated silt bed, showing subvertical burrows extending from overlying bioturbated mudstone. Sample 5H3, Upper Elton Beds near Perton. SO 592394.

All figures are untreated rock slabs cut vertically to bedding; scales equal 1 cm.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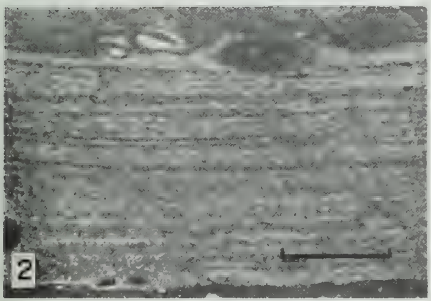
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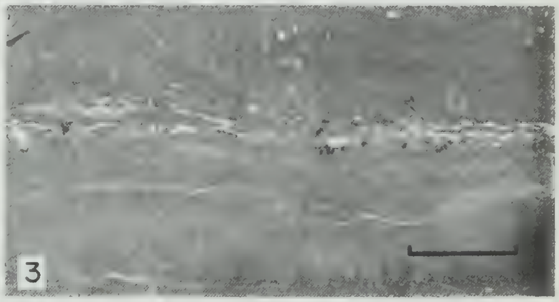
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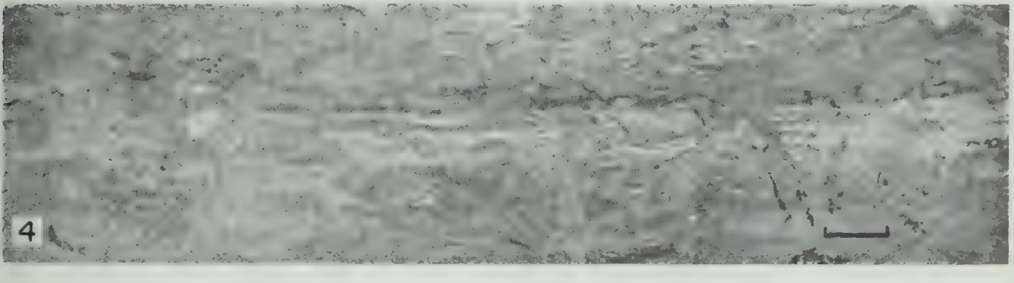
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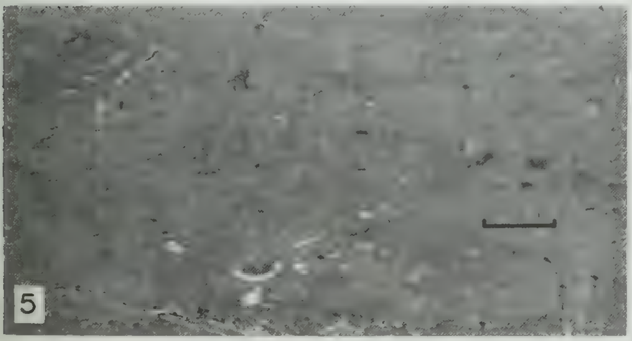
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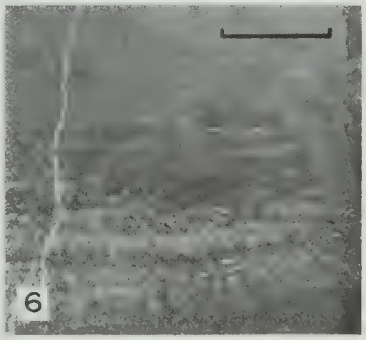
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Non-bioturbated, primary bedding composes about 4% of the facies. Isolated beds of laminated siltstone are identical to those of the mudstone facies (Pl. 1, fig. 2). Lenticular beds of shells and shell fragments also occur, and are generally 1–4 cm thick and less than 2 m in apparent length. Bases of beds are sharp erosional contacts. Upper surfaces are intensely bioturbated, with stringers of shell debris incorporated into the overlying siltstone (Pl. 1, fig. 1). Very thin layers of shell fragments and convex-upwards shells lying parallel to the bedding also occur throughout the facies, showing many burrow disruptions (Pl. 1, fig. 3). They have an average frequency of about 1 layer per 40 cm of vertical section.

Calcisiltite facies

The calcisiltite facies forms the Lower Bringewood Beds in the immediate area of Ledbury, and is a very local lateral equivalent of the bioturbated siltstone facies. It is 53 m thick, and is shown in detail in Fig. 19, p. 217. The sediment consists of very calcareous siltstone and gradational silty and argillaceous limestone. One thin section of the purest limestone is composed of 89% microsparite, 3% bioclasts, 7% mica and argillaceous material and 1% quartz grains. Most sediment, however, contains at least 50% terrigenous material.

Bioturbation is apparent throughout the calcisiltite facies by scattered, variably orientated shell material and the presence of *Chondrites*. Flat continuous weathering planes, traceable for several metres laterally, probably represent the original bedding. These planes contain local concentrations of convex-upwards shells. Thin, lenticular shell beds, identical to those of the bioturbated siltstone facies, also occur. Minor stratigraphic variations within the calcisiltite facies are shown in Fig. 19.

'Aymestry Limestone' facies

This facies comprises the Upper Bringewood Beds and basal Lower Leintwardine Beds of the Woodbury Quarry, Ledbury and Perton areas, and reaches 15 m in thickness. It is also present at the type boundary of these two units near Ludlow. One thin section from sample 5D11, from the Upper Bringewood Beds at Perton Quarry, consists of 93% microsparite, 2% quartz grains and 1% mica and argillaceous material. The limestone is generally siltier, however, and shows all gradations to highly calcareous siltstone. Microsparite nodules comprise 15% of the facies by volume.

In unweathered exposures, the only definition of bedding in this facies are thin bentonites, which divide the limestone into layers 0·5–2 m thick. This thick-bedded aspect of the facies can be seen in the Upper Bringewood Beds shown in Pl. 3, fig. 2 (p. 195). Sedimentary structures have not been observed within these layers, except for a single parallel-laminated bed observed at Woodbury Quarry. This may reflect intense bioturbation. Shells are usually rare and widely scattered, but sometimes occur in concentrated layers immediately below bentonites.

This facies extends upwards into the basal few metres of the Lower Leintwardine Beds, as determined by faunal content. These occurrence are distinguished, however, by beds of concentrated shell material and parallel-laminated, silty limestone with sharp erosional bases. Although compositionally like strata of the Upper Bringewood Beds, the limestones of the basal Lower Leintwardine Beds show periodic higher energy conditions. They grade upwards into the coquinoid siltstone facies, which contains similar sedimentary structures.

The preceding description of the 'Aymestry Limestone' facies applies only to the Woodbury Quarry, Ledbury and Perton areas, and section 2D near Ludlow. Upper Bringewood carbonates west of Ludlow, in the area between View Edge and Aymestrey, are distinguished by a dominant, sparry texture, common sedimentary structures, and common shell beds. These carbonates represent a more high-energy environment, and are located along a postulated shelf-edge barrier zone. Two depositional facies occur in this area, one characterized by common trough cross-bedding and deflation deposits of *Kirkidium*. The second facies is developed as thin tabular beds with great lateral continuity, and probably represents down-slope redeposition of carbonate sediment. A facies analysis of Upper Bringewood carbonates throughout the northern Welsh Borderland will be detailed in a separate publication.

Coquinoid siltstone facies

The coquinoid siltstone facies forms the Leintwardine Beds and Whitcliffe Beds, and reaches 80 m in thickness. Clay content is low, and silt and shell material predominate. Average grain size of quartz is 0·03–0·04 mm, and about 10% of grains are of fine sand grade (Fig. 4). Minor vertical variations in texture are common.

Bioturbation is present throughout the facies, varying from discrete burrows in laminated beds to intricate, deformative mottling (Pl. 2, figs 1, 2, 5). Primary bedding has been destroyed in about 75% of measured sections. In general, however, bioturbation is not as intense as in other terrigenous facies, and small traces of lamination commonly remain.

Shell beds comprise an average of 3% of the facies, but are highly variable in abundance between sections (Table 4). Shell material accounts for 5–20% of bed volume, and may be parallel to bedding and convex-upwards, or without consistent orientation (Pl. 2, fig. 4). Quartz grains in shell beds reach larger sizes than in the surrounding sediment, and may exceed 0·2 mm. Rounded intraformational pebbles below 5 cm in size occur in shell beds of the Lower Leintwardine Beds.

The shell beds have erosional bases which are usually flat and parallel to the general stratification. Occasionally they fill small scours less than 5 cm deep and 20 cm across. The beds are variable in thickness (Table 4), usually below 5 cm, and form small sheets, thickest centrally and thinning towards their margins; they usually extend less than 5 m laterally. Where bioturbation is minimal, shell beds form the basal layers of laminated sheets of silt (Pl. 2, fig. 4). Upper boundaries of shell beds are marked by a sharp reduction in shell density, their matrix being sometimes in textural continuity with the overlying laminated silt. As shell beds pinch out laterally, they are replaced by laminated siltstone, and a laminated siltstone sheet may have several separate lenses of shells along its base. All gradations exist between single basal shell layers and shell beds up to 10 cm thick. Bioturbation has often destroyed the laminations above shell beds, and burrowing may disrupt their upper contacts.

Table 4 Stratigraphic measurements of shell beds in the coquinoid siltstone facies. ULB – Upper Leintwardine Beds; LLB – Lower Leintwardine Beds; UWB – Upper Whitcliffe Beds; LWB – Lower Whitcliffe Beds; WB – Whitcliffe Beds, undifferentiated

section number	1B	1C	2B	2C	3A	3A	4A	5A	5C
stratigraphic unit	ULB	LLB	UWB	LWB	WB	LLB	LLB	UWB	LLB
number of shell beds	6	14	9	4	5	17	27	5	9
mean bed thickness (cm)	6·8	4·2	1·8	2·0	3·6	2·5	4·8	1·8	3·3
thickness of section (m) ÷ number of shell beds	0·65	0·46	1·16	5·74	6·00	0·97	0·49	1·22	0·64
shell beds as percentage of stratigraphic thickness	10·5	9·1	1·5	0·3	0·6	2·6	9·7	1·5	5·2

Laminated siltstone forms 22% of the facies (Pl. 2, fig. 1). Laminae are usually 0·5–1 mm thick, but may reach thicknesses of 3 mm. They consist of alternations of quartz-dominated silt and clay-rich, mica-dominated silt. Laminae consist locally of pure, uniformly-orientated biotite. Laminated siltstone forms tabular continuous sheets with nearly flat erosional bases. Where not disrupted by bioturbation, the sheets are continuous across outcrops reaching 10 m in lateral extent. Some detailed stratigraphic distributions of these beds are shown in Fig. 10 (p. 201) and Figs 16, 18 and 20 (pp. 213–218).

In the Lower Leintwardine Beds, Upper Leintwardine Beds and Lower Whitcliffe Beds, laminated siltstone usually occurs as isolated sheets within sequences of bioturbated siltstone. These sheets are less than 10 cm thick and have intensely bioturbated tops. In Perton Quarry, however, bentonites have preserved upper surfaces of sheets with symmetrical ripple marks 1–2 cm in height and 20–30 cm in apparent length. Sheets are formed internally of flat to slightly wavy parallel lamination. Small ripple bedding, as defined by Reineck & Singh (1973), is also present.

The Upper Whitcliffe Beds contain more laminated siltstone, with smaller intervals of bioturbated sediment (Figs 16 and 20). Thin, laminated sheets like those described above occur. Other laminated sheets reach 50 cm in thickness. These have nearly flat erosional bases and bioturbated tops. Internally, they consist of several distinct beds with erosional contacts, often showing a number of basal shell layers and two or three stages of minor burrowing; often beds are cut out completely at the base of other beds. They contain wavy, parallel lamination or small ripple bedding. Cross sets are generally 2 cm or less thick, of both planar and trough form, and orientated at less than 5° to the general stratification.

Another type of laminated siltstone sheet reaches 20 cm in thickness and contains parallel, even lamination throughout. In contrast to other beds, these sheets may completely lack bioturbation. Siltstone sheets containing convoluted laminae are also present. One such sheet, which defines the base of the Upper Whitcliffe Beds at Ludlow, has a lateral extent of at least 500 m (Holland *et al.* 1963).

The storm-related model of shelf sedimentation

Gadow & Reineck (1969) and Reineck & Singh (1972) described modern shelf sediments, in the Mediterranean and North Sea, which consist of bioturbated mud with interbedded sheets of laminated sand and silt. Laminated sheets have nearly flat erosional bases, infrequent basal shell layers and bioturbated upper surfaces. They decrease in thickness with increasing distance from shore. Similar beds from the Georgia shelf were described by Howard & Reineck (1972).

These authors proposed a storm-related model of shelf sedimentation. Normal shelf deposition consists of settling of suspended silt and clay which is thoroughly reworked by burrowing. During storms, sand or silt is eroded from nearshore areas and transported onto the shelf by retreating waves and ebb currents. In the southern North Sea, sand from tidal flats is carried and redeposited as far as 50 km out onto the shelf (Gadow & Reineck 1969). Minor erosion of the shelf surface, sometimes accompanied by emplacement of a shell layer, is followed by rapid settling of sand or coarse silt as tabular, laminated sheets. This may be followed by rapid settling of suspended mud. Reineck & Singh (1972) considered the sand or coarse silt to be transported in a turbidity-current fashion as 'clouds' of material which settle as the energy of transport decreases. Goldring & Bridges (1973) reviewed the general features of laminated sheets in ancient and modern shelf sediments, and also concluded that very rapid turbidity-current type deposition is involved.

Storm-related models of sedimentation have also been applied to Jurassic and Devonian shell beds by Brenner & Davies (1973) and Bowen, Rhoads & McAlester (1974). These shell beds form erosively-based sheets several cm thick within finer-grained, often bioturbated sediment. In the

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Plate 2

Coquinoid Siltstone Facies

Fig. 1. Portion of a tabular bed of cross-laminated silt, with large subvertical burrow. Section 1C, Lower Leintwardine Beds near Millichope Park. SO 529890.

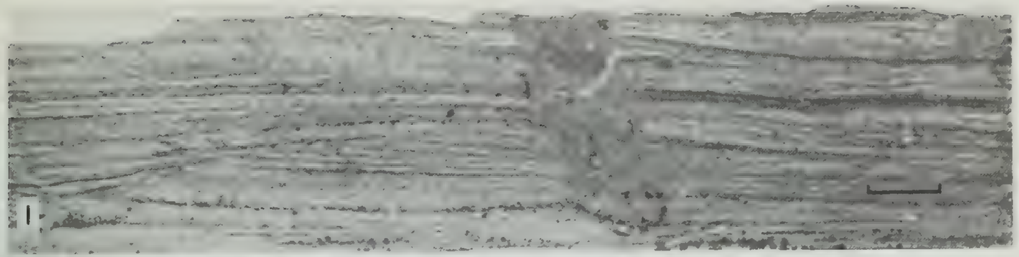
Fig. 2. Small-scale relations of laminated silt, bioturbated silt and bioclastic layers, showing incipient destruction of bedding by burrowing. Section 5A, Upper Whitcliffe Beds, Perton. SO 597403.

Fig. 3. Detail of quarry face showing dominantly tabular bedding in the uppermost portion of the Coquinoid Siltstone Facies. Most of the beds shown represent 'amalgamated sheets' of laminated siltstone. Section 5A, as last.

Fig. 4. Bioclastic layer resting on bioturbated silt and overlain by laminated silt. The shelly layer and laminated silt are attributed to rapid sedimentation during a single storm event. Sample 5A4, Upper Whitcliffe Beds, Perton. SO 597403.

Fig. 5. Burrowing in a laminated silt bed, showing vertical sections of the trace fossil *Chondrites*. Sample 4A28, Upper Leintwardine Beds, Frith Wood, near Ledbury. SO 722402.

Figures 1, 2, 4 and 5 are untreated rock slabs cut vertically to bedding; scales equal 1 cm.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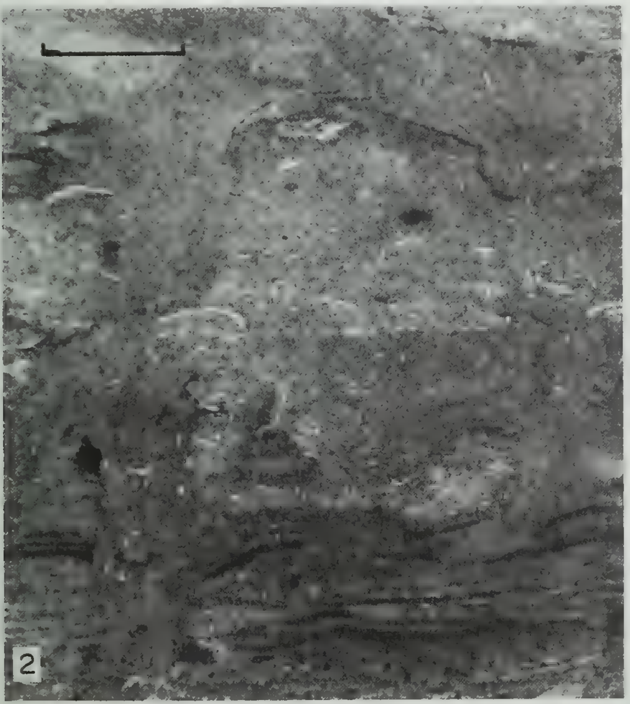
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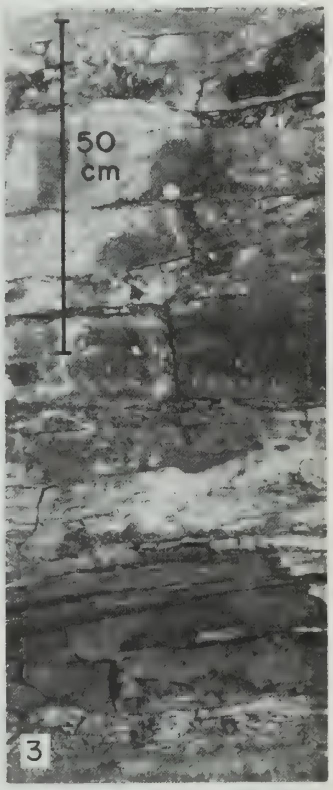
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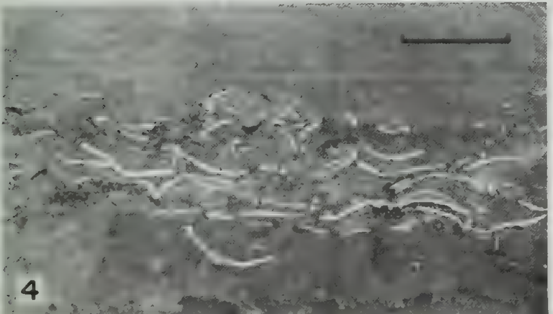
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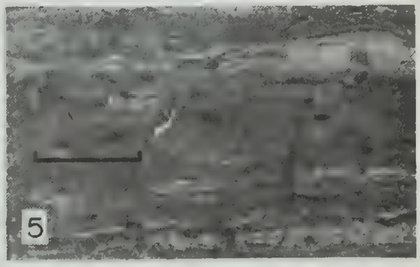

5

Jurassic examples, shell beds contain larger detrital grains than the surrounding sediment, and in the Devonian example they are overlain by laminated sheets of siltstone. The shell beds represent higher depositional energies than the sediments with which they are intercalated, and Brenner & Davies (1973) and Bowen *et al.* (1974) related them to rapid transport and deposition during storms. Bridges (1975) has made similar interpretations for shell beds at the base of laminated sandstones in Llandovery shelf deposits.

Application of the model to Ludlow shelf sediments

The Ludlow terrigenous facies in the Welsh Borderland are directly comparable to modern shelf sediments in consisting of an alternation of bioturbated silt and clay with coarser-grained, laminated sheets of silt (Pl. 1, fig. 2). Laminated siltstone sheets in Ludlow facies represent rapid, turbidite-type deposition during storms. Shell beds are genetically related deposits, and represent the traction load, or initially-settling coarse fraction, during mass transport of silt. Emplacement of sheets of shells and laminated silt was accompanied by very little erosion of the Ludlow shelf. This is indicated by their flat, generally non-scoured bases, and also by faunal evidence. As discussed later, shell beds consist almost wholly of epifauna, with significantly fewer infaunal shells than in bioturbated sediment. Lingulids, for example, were very rarely scoured from their burrows on the Ludlow shelf. In the bioturbated siltstone facies, 95% of observed lingulids occur in vertical life position (N = 55), and 81% are in life position in bioturbated sediment of the coquinoid siltstone facies (N = 26). These relations indicate that sediment deposited in the study area remained essentially in place. Palaeocurrent directions indicate that sources of the storm-derived silt were probably from the south and east (Bailey & Reese 1973).

Terrigenous deposits of the measured sections show a stratigraphic succession from the mudstone facies, through the bioturbated siltstone facies to the coquinoid siltstone facies (Fig. 3). This succession shows the following trends:

1. Upward decrease in clay content, shown relatively in Table 5 by the increase in volumetric proportion of quartz grains.

Table 5 Quartz composition of Ludlow terrigenous facies, based on 100–250 point counts on one thin section per sample. S – sample number; Q – percentage of detrital quartz. The general increase in quartz percentage from the mudstone facies to coquinoid siltstone facies is a general reflection of a decreasing amount of clay within sediments

mudstone facies Elton Beds		bioturbated siltstone facies Bringewood Beds		coquinoid siltstone facies Leintwardine and Whitcliffe Beds	
S	Q	S	Q	S	Q
1E6	20%	1D10	34%	2B3	59%
4C1	24%	2E1	27%	2C7	55%
		3A92	27%	3A11	45%
		5E3	26%	3A14	49%
		5F1	21%	5A4	49%

2. Upward increase in average silt size, with sand appearing high in the succession (Fig. 4).
3. Upward decrease in bioturbation, from over 99% destruction of primary sedimentary structures in the mudstone facies to about 75% destruction in the coquinoid siltstone facies.
4. Upward increase in frequency and thickness of laminated sheets of siltstone and shell beds.
5. Upward trend towards reworking and sediment dilution of bentonites.

These trends indicate a general increase in sedimentation rate, energy level and proximity to sediment source. The mudstone facies represents a distal, shelf, quiet environment, as indicated by fine grain size, intense bioturbation and stratigraphic position at the initiation of a marine deepening in the Welsh Borderland (Hurst 1975*a*). Sedimentation appears to have been dominantly from suspension, and the rarity of laminated siltstone sheets indicates lack of storm influence and distance from sources of redeposited sediment. The bioturbated siltstone facies also represents a distal shelf environment removed from sediment sources, but increasing agitation is apparent by frequent concentrations of shell material. These concentrations are compared to 'swell lags' in following sections, and related to the distal passage of wave motion (but not transported sediment) during storms.

The coquinoid siltstone facies completes the Ludlow terrigenous cycle, and represents a proximal shelf environment, nearer to the sediment source, and subject to frequent storm sedimentation. The culmination of this trend is seen in the Upper Whitcliffe Beds, where convolute laminations and the predominance of laminated siltstone sheets indicate the highest sedimentation rates. The amalgamated sheets of siltstone in this interval probably represent close proximity to sources of redeposited sediment (Goldring & Bridges 1973).

Significance of the laminated shale facies

The laminated shale facies is laterally equivalent to the mudstone facies (Fig. 3), and also represents a very low-energy, distal shelf environment. Although identical in texture and composition to the mudstone facies, it differs in its lamination and rarity of bioturbation. Rhoads & Morse (1971) identified very low oxygen concentrations as a major restrictive factor for bioturbating organisms of offshore shelves. Where concentrations of bottom oxygen reach their lowest levels in the Santa Barbara Basin and Gulf of California, shelf muds preserve complete lamination, and have few burrowing organisms (Emery & Hülsemann 1962; Calvert 1964). Low oxygen level and rarity of burrowers can be considered a major environmental distinction of the Ludlow laminated shale facies.

The relation of Ludlow carbonates to the terrigenous shelf succession

The 'Aymestry Limestone' facies of the Upper Bringewood Beds and basal Lower Leintwardine Beds in sections studied here is an interruption of the terrigenous succession discussed above (Fig. 3). From Ludlow to the Ledbury area, the 'Aymestry Limestone' facies can be characterized as quiet-water and offshore, but otherwise shows no sedimentary features diagnostic of a specific environment. Its fauna, the *Atrypa reticularis* – coral Association, is a depauperate assemblage compared with the underlying bioturbated siltstone facies, which suggests some restrictive type of environment.

According to the correlation presented in Table 1, p. 181, these carbonates are equivalent in age to high-energy, *Kirkidium*-bearing limestones of the shelf edge area. Alexander (1936) and Lawson (1973*a*) considered these shelf-edge limestones as very shallow-water in nature and possibly forming a low submarine ridge. This interpretation is supported by the sedimentary observations given earlier. From these relations, we can conclude that the low-energy 'Aymestry Limestone' facies of the study area represents a back-barrier deposit, formed under deeper, quieter water than the high-energy limestones at the relief edge.

Phipps & Reeve (1967) and Lawson (1973*a*) have considered Upper Bringewood carbonates as the shallowest part of a Lower Ludlow shoaling cycle, followed by transgressive or deeper-water conditions during deposition of the Lower Leintwardine Beds. This interpretation is valid for the shelf edge regions around Leintwardine and Aymestrey, outside the present study area. Interpretation of an Upper Bringewood shallowing, followed by deepening in Lower Leintwardine times, is not valid for the areas considered in this study, however, and ignores important differences between shelf edge and inner shelf areas. These differences may be listed as follows:

Shelf edge (Leintwardine, Aymestrey areas)	Inner shelf (Woodbury Quarry, Perton areas)
Upper Bringewood Beds comprising carbonates with high-energy sedimentary structures and abundant sparite	Upper Bringewood Beds of massive, low-energy carbonate of microsparite and argillaceous material
Upper Bringewood Beds end with an erosional surface at the base of the overlying Lower Leintwardine Beds, with abrupt faunal change	Continuous sedimentary and faunal transition, with no erosional breaks between the Upper Bringewood Beds and Lower Leintwardine Beds
Basal Lower Leintwardine Beds often very clay rich, and often with relatively poor bioturbation and partially preserved, parallel lamination	Lower Leintwardine Beds typical of coquinoid siltstone facies described earlier, continuing terrigenous sedimentary trends from the Lower Bringewood Beds

The low-energy 'Aymestry Limestone' facies of the study area appears to represent a pause in the progression of terrigenous shelf deposits over the Welsh Borderland, related to reduced terrigenous supply and local elevation of a barrier zone at the shelf edge. These low-energy carbonates grade upward into the coquinoid siltstone facies of the Lower Leintwardine Beds, which continues the general progressionary trend of terrigenous facies. Lawson (1973*a*) has referred to a basal conglomerate of regional development as the beginning of Lower Leintwardine deposition. An uninterrupted sedimentary transition from the Upper Bringewood Beds to the Lower Leintwardine Beds can be observed in the type section near Ludlow and at Woodbury Quarry and Perton Quarry (Pl. 3, fig. 2). Measurement of these sections cm by cm has failed to reveal a basal Lower Leintwardine conglomerate. Several laminated siltstone sheets in the lowest several metres of the Lower Leintwardine Beds in Woodbury and Perton Quarries include scattered pebbles of limestone and calcareous siltstone. These pebbles almost certainly relate to minor intraformational erosion during storms. They do not represent a discrete basal conglomerate, and do not indicate an abrupt change in regional depositional conditions.

Shell occurrence

Disturbed neighbourhood assemblages and transported assemblages

Ludlow shell occurrences can be assigned to two general taphonomic categories defined by Scott (1974). Transported asemblages consist of shells which have been mechanically deposited during sedimentation. This term refers to a process, and has no implicit connotations of distance or ecological mixing. In Ludlow sediments, these assemblages consist of storm-related shell beds as described earlier, associated with erosional surfaces and laminated sheets of siltstone. Examples are shown in Pl. 1, fig. 1 and Pl. 2, fig. 4. Other transported assemblages are formed of convex-upwards shells which are closely packed in layers parallel to bedding (Plate 4, p. 225).

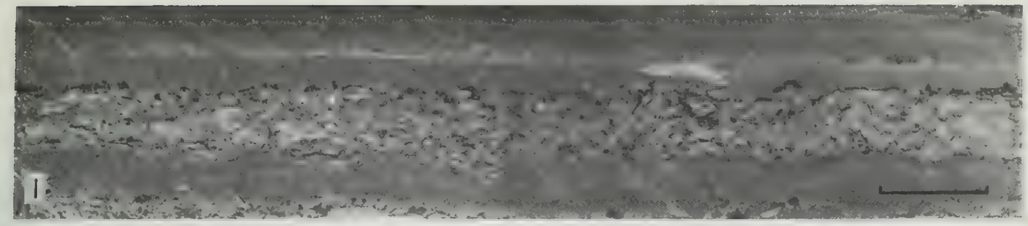
Scott (1974) defined a disturbed neighbourhood assemblage as fossils which have been shifted from their life positions, but not significantly moved or mixed ecologically. Bioturbation is the common agent of disturbance. These assemblages have been identified in this study by a dispersed, inconsistently orientated scatter of shells within bioturbated sediment (Pl. 1, fig. 5). This is the most common type of shell occurrence in Ludlow shelf sediments.

Plate 3

Fig. 1. Vertical saw-cut section of the Ludlow Bone Bed from the type locality at Ludford Lane, Ludlow. In this sample the bone bed is developed as two layers of bone material, the lower one being barely visible in the lower left of the figure. Note the sharp contacts of the upper layer of bone material, and the overlying parallel-laminated silt; compare with Pl. 2, fig. 4. These features are indicative of storm-related redeposition of sediment rather than in-place accumulation of the bone material, as discussed in text. Scale in figure indicates 1 cm.

Fig. 2. Perton Quarry (designated as section 5D in this report), showing the Upper Bringewood Beds ('Aymestry Limestone' Facies) and Lower Leintwardine Beds (Coquinoid Siltstone Facies). Note the laterally continuous, tabular character of bedding. Photograph by Charles Aithie.

1



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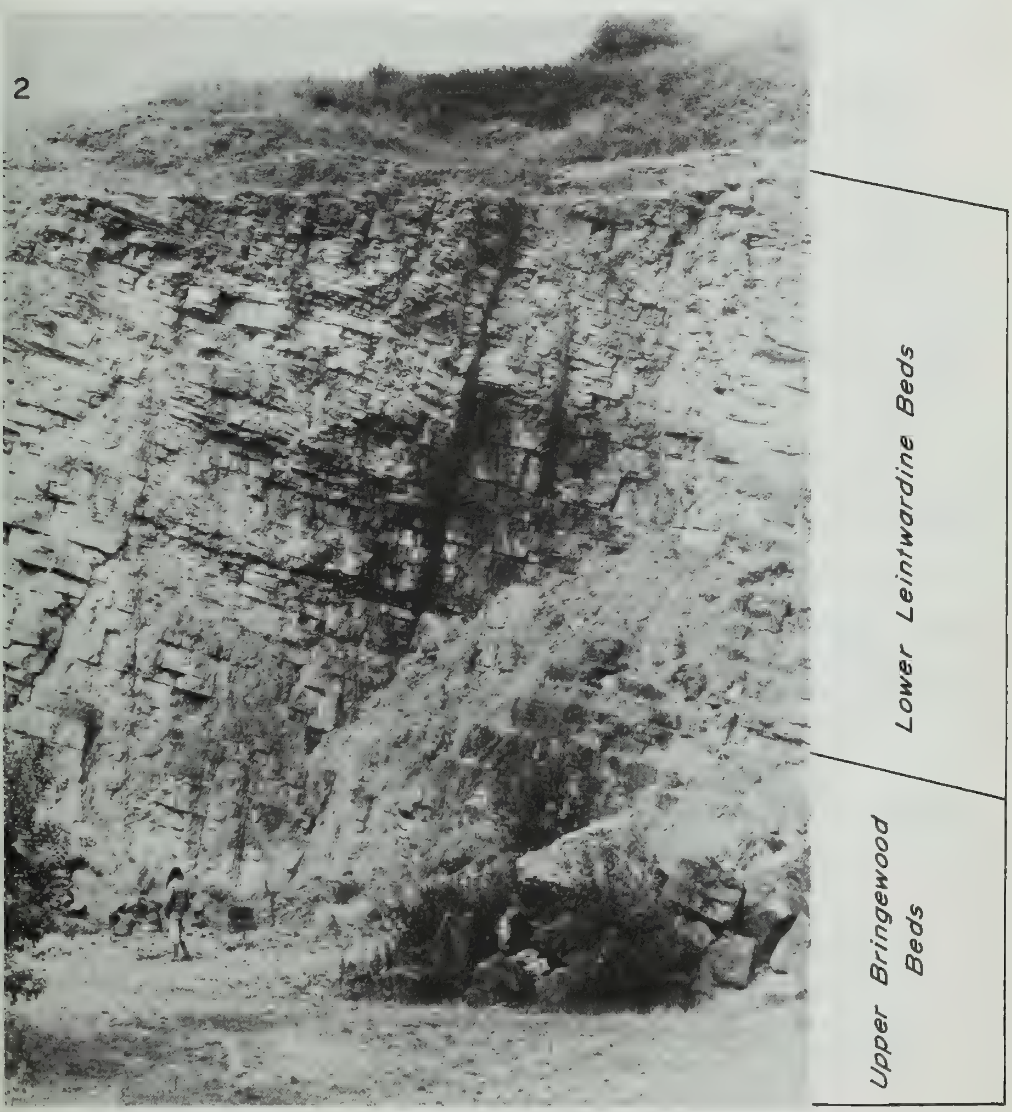

Lower Leintwardine Beds
Upper Bringewood Beds

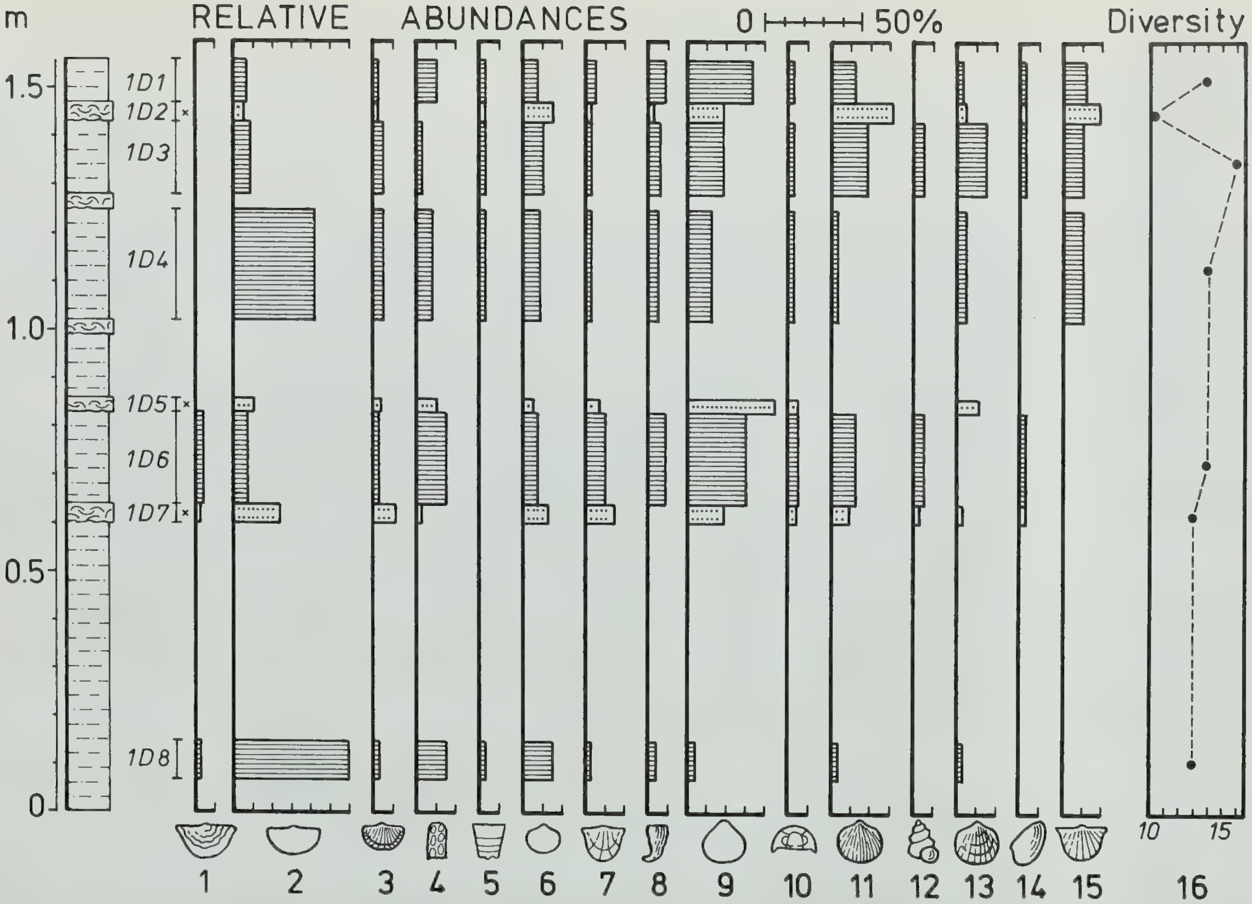


Fig. 5 Section 1D, Lower Bringewood Beds, Millichope, containing the *Mesopholidostrophia laevigata* Association. Shell beds are shown schematically, and occur within bioturbated siltstone. Note that transported assemblages from shell beds show no major faunal differences from disturbed neighbourhood assemblages in bioturbated siltstone. 1 – *Leptaena depressa* and *Lepidoleptaena* sp.; 2 – *Mesopholidostrophia laevigata*; 3 – *Amphistrophia funiculata*; 4 – bryozoa; 5 – cephalopods; 6 – various brachiopods; 7 – *Strophonella euglypha*; 8 – trochoid corals; 9 – *Gypidula lata*; 10 – trilobites; 11 – *Isorthis clivosa*; 12 – gastropods; 13 – *Atrypa reticularis*; 14 – bivalves; 15 – *Leptostrophia filosa*; 16 – rarefaction index for number of species at 50-individual sample size. Mean size of samples = 104 individuals.

Shell occurrence in the mudstone facies and laminated shale facies

Sections of the mudstone facies show a continuous stratigraphic occurrence of disturbed neighbourhood assemblages of shells. Shell material is evenly scattered through sediment in many orientations, as shown in Pl. 1, fig. 5. Rare lingulids and endobyssate bivalves remain in burrowing position, but life orientations and small-scale distributions of other forms have been destroyed by intense bioturbation. The pattern of long-term stratigraphic persistence of disturbed neighbourhood assemblages has been defined as the vital-pantostrate biofacies by Shäfer (1972). He considered the biofacies to preserve a complete in-place history of communities of fine-grained, quiet bottoms. This is corroborated in the mudstone facies by gradual stratigraphic cycles in the abundance of different species.

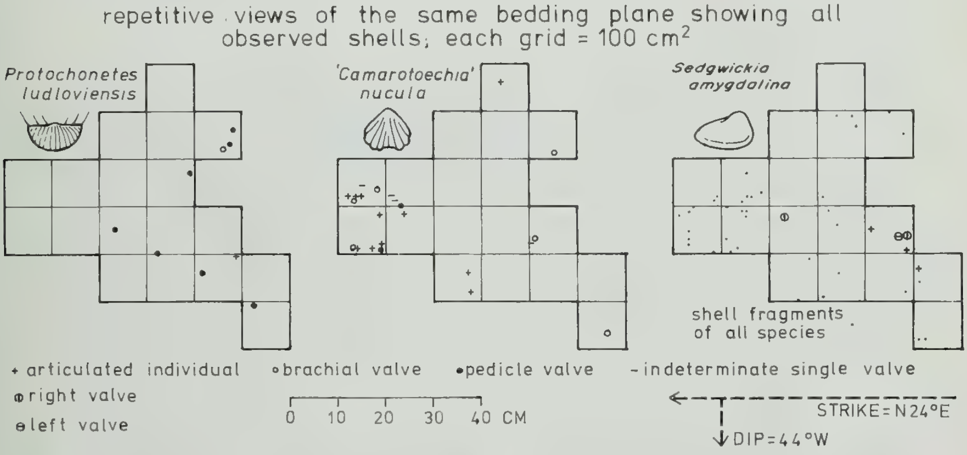

repetitive views of the same bedding plane showing all observed shells; each grid = 100 cm²
Protochonetes ludloviensis
'Camarotoechia' nucula
Sedgwickia amygdalina
shell fragments of all species
+ articulated individual
○ brachial valve
● pedicle valve
- indeterminate single valve
⦶ right valve
⊖ left valve
0 10 20 30 40 CM
STRIKE = N24°E
DIP = 44°W

Fig. 6 Faunal variation in a disturbed neighbourhood assemblage of the *Protochonetes ludloviensis* Association in the Whitcliffe Beds of section 4A, Ledbury. This assemblage occurs 50·83 m above the base of the section, and can be located by this reading in Fig. 11.

The laminated shale facies contains rare intervals of intensely bioturbated sediment with a shell occurrence like that of the mudstone facies. Most of the laminated shale facies, however, contains only graptolites, cephalopods and other pelagic organisms, with very rare benthic shells. Shäfer (1972) discussed this type of shell occurrence as the letal-pantostrate biofacies, and related it to a poorly oxygenated bottom environment.

Shell occurrence in the bioturbated siltstone facies, calcisiltite facies and 'Aymestry Limestone' facies

Disturbed neighbourhood asemblages in bioturbated sediment are the main type of shell occurrence in these facies, and can be seen below the shell bed in Pl. 1, fig. 1. Transported assemblages occur as rare erosively-based shell beds, as also shown in Pl. 1, fig. 1. The fauna in transported shell beds does not differ from that in surrounding disturbed neighbourhood assemblages. This is shown graphically in Fig. 5, and discussed in the next section, p. 200.

Another type of transported assemblage consists of very thin bedding-parallel layers of closely-packed shells and shell fragments. A vertical section of one of these layers is shown in Pl. 1, fig. 3, and upper surfaces of layers are illustrated in Pl. 4, figs 1–5. These layers are often no thicker than a single shell, with no associated erosional surface, and have identical bioturbated sediment above and below. Shells are both whole and disarticulated, variably broken and unabraded. Faunal content is identical to surrounding disturbed neighbourhood assemblages. The shell layers probably represent 'swell lags', which are discussed below.

In general, shell occurrence in these three facies represents an intermediate taphonomic state between relatively in-place faunas of the underlying mudstone facies and more disturbed, often transported shell occurrences of the overlying coquinoid siltstone facies.

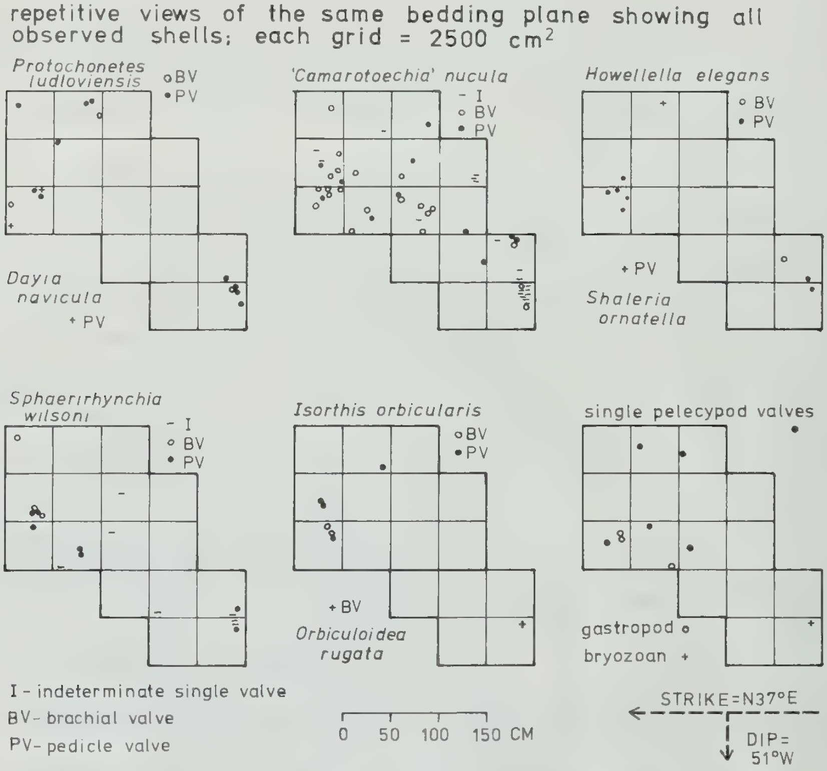

repetitive views of the same bedding plane showing all observed shells; each grid = 2500 cm²
Protochonetes ludloviensis
o BV
• PV
Dayia navicula
+ PV
'Camarotoechia' nucula
- I
o BV
• PV
Howellella elegans
o BV
• PV
+ PV
Shaleria ornatella
Sphaerirhynchia wilsoni
- I
o BV
• PV
Isorthis orbicularis
o BV
• PV
+ BV
Orbiculoidea rugata
single pelecypod valves •
gastropod o
bryozoan +
I - indeterminate single valve
BV - brachial valve
PV - pedicle valve
0 50 100 150 CM
STRIKE=N37°E
DIP= 51°W

Fig. 7 Faunal variation in a disturbed neighbourhood assemblage of the *Sphaerirhynchia wilsoni* Association in the Lower Leintwardine Beds of section 4A, Ledbury. This plane is sample 4A42, which is shown stratigraphically in Fig. 10. The closely-packed shells in the two lower right grids are a small transported assemblage.

Shell occurrence in the coquinoid siltstone facies

Disturbed neighbourhood assemblages occur throughout bioturbated sediment of this facies, and have been investigated by inscribing grids on small areas of bedding surface. One example is shown in Fig. 6, where a discrete cluster of endobyssate bivalves occurs in one small area, separated by about 25 cm from a cluster of articulated and separate rhynchonellid valves. Both clusters are probably very close to their life positions, and their distributions suggest small-scale clumping of conspecific populations. Fig. 7 shows the distribution of a more scattered, disturbed neighbourhood assemblage. In this example, the slight differences in distribution of species may be a blurred reflection of original areas of life. However, the brachiopods are wholly disarticulated, and some species are represented mainly by pedicle valves.

Transported assemblages in the coquinoid siltstone facies are frequently represented by thin bedding-parallel layers of shells not associated with erosional surfaces. These are illustrated in Pl. 5, figs 1–4. Fig. 8 shows a grid analysis of faunal distribution in a thin layer of closely-packed shells. Significant lateral variation occurs in the composition of this shell layer. For example, Grid D in Fig. 8 contains a nearly equal mixture of '*Camarotoechia*', *Hyattidina*, *Salopina*, *Sphaerirhynchia* and *Isorthis*, while Grid K, 2 m away, is dominated by '*Camarotoechia*', *Salopina*, bivalves and ostracods. This small-scale variation may indicate that transport during formation of the shell layer was limited, partially maintaining original distributions. It probably does not result from different hydrodynamic properties of the various taxa, which would be nearly identical in the case of *Isorthis* and *Salopina*.

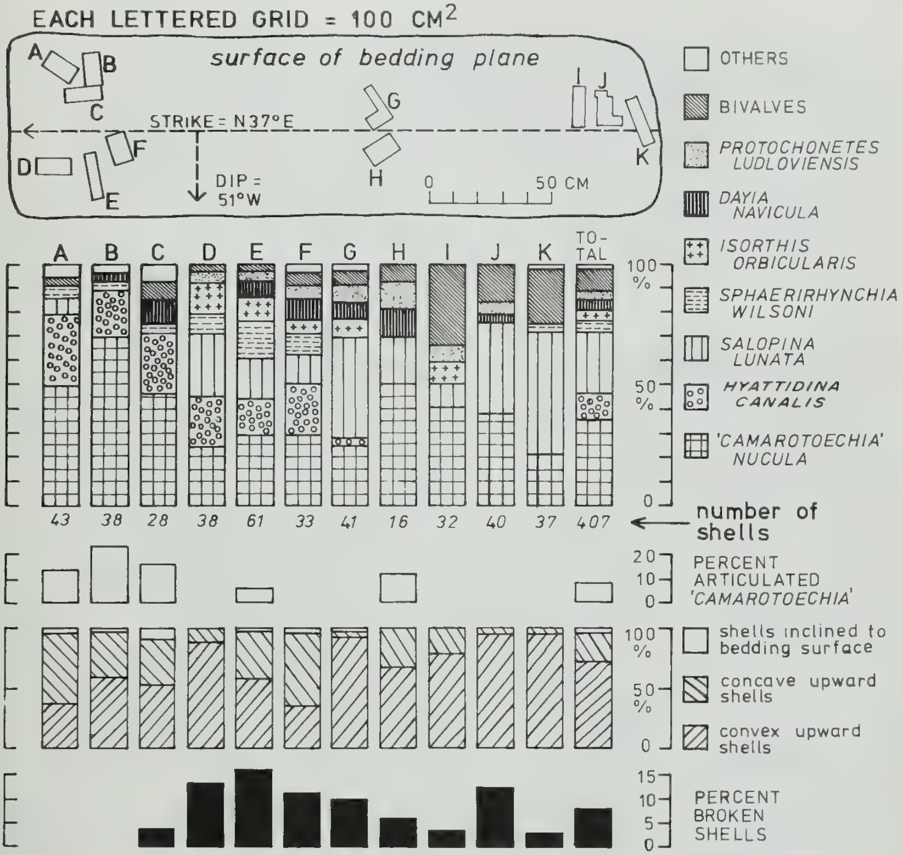


Fig. 8 Faunal variation in a very thin 'swell-lag' layer of transported shells, which covers the entire bedding plane and not just the sampled grids. This example is from the *Sphaerirhynchia wilsoni* Association of the Lower Leintwardine Beds, section 4A, and is shown in Fig. 10 as sample 4A45.

The swell lag mechanism discussed by Brenner & Davies (1973 : fig. 12) is a probable cause of the thin shell layers like that described above. Swell lags may form in fine-grained shelf sediment when storm-produced waves rework the upper shelf surface, suspending shells and sediment grains. Shells then settle first as a concentrated, coarse fraction, without significant lateral movement.

Storm-deposited beds of transported shells in the coquinoid siltstone facies have been described in the previous section, and are shown in Pl. 2, fig. 4. Faunal distribution on the upper surface of a shell bed is shown in Fig. 9. In contrast to the previous example, faunal content of the bed is fairly uniform over several metres, suggesting thorough mixing during transport. A graphic comparison of fauna between some transported shell beds and disturbed neighbourhood assemblages in the coquinoid siltstone facies is given in Figs 10 and 11. Faunal differences between the two types of assemblages and their implications will be discussed in the next section.

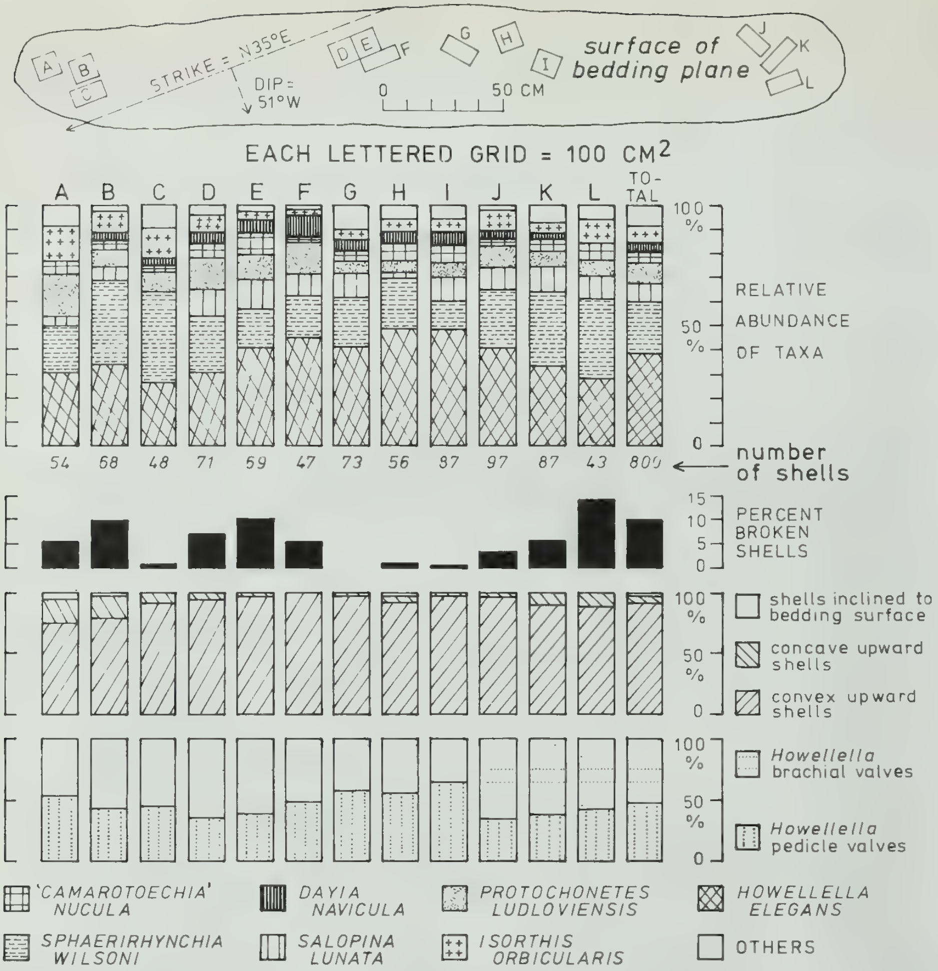


Fig. 9 Faunal variation on the upper surface of a 5 cm thick shell bed, shown as sample 4A44 in Fig. 10. From the *Sphaerirhynchia wilsoni* Association, Lower Leintwardine Beds, section 4A.

The alternation of transported and disturbed neighbourhood assemblages in the coquinoid siltstone facies represents the vital-lipostrate biofacies of Shäfer (1972). Nearly in-place communities are recorded in bioturbated sediment, biological information is lost at erosional surfaces, and transported faunas are introduced during storms. Shäfer's model for the vital-lipostrate biofacies states that benthic communities are killed *en masse* by very rapid storm sedimentation and erosion. This phenomenon affected faunas living during deposition of the coquinoid siltstone facies. Infaunal lingulids and bivalves occur in life position beneath storm-deposited, laminated siltstone sheets, and show no evidence of escape trails, while epifauna are found as concentrated, transported layers along the base of the sheets.

Analysis of shell transport

Method of analysis

This section analyses the effects of shell transport in the bioturbated siltstone facies and coquinoid siltstone facies. Transported assemblages have been identified on sedimentological not faunal

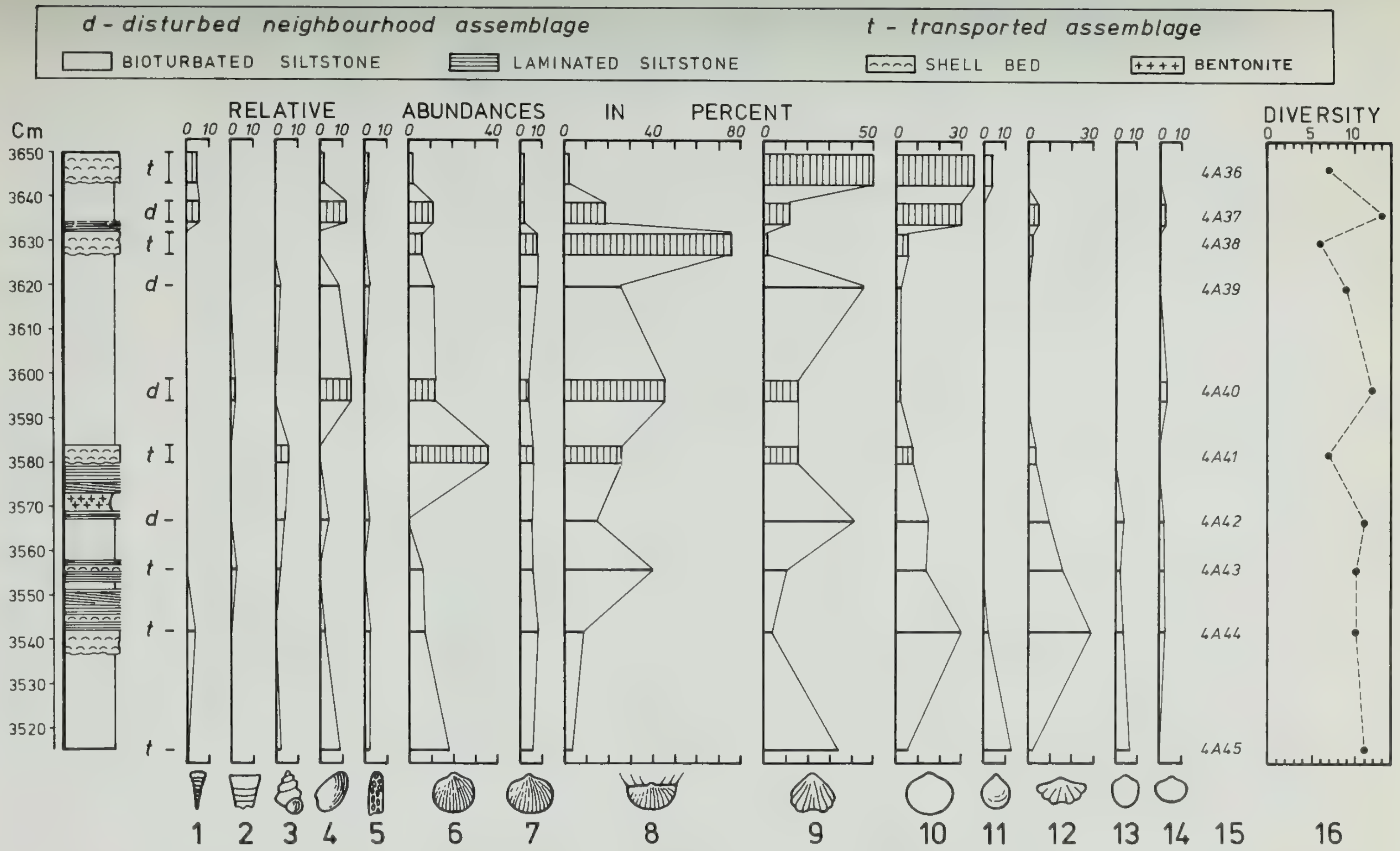


Fig. 10 Small-scale stratigraphic variation in the *Sphaerirhynchia wilsoni* Association, Lower Leintwardine Beds, section 4A, Ledbury, based on a mean count of 117 individuals per sample. Note the rarity of molluscs in transported assemblages. 1 – *Tentaculites tenuis* and *Cornulites serpularius*; 2 – cephalopods; 3 – *Cyclonema corallii*; 4 – bivalves; 5 – bryozoa; 6 – *Salopina lunata*; 7 – *Isorthis orbicularis*; 8 – *Protochonetes ludloviensis*; 9 – '*Camarotoechia*' *nucula*; 10 – *Sphaerirhynchia wilsoni*; 11 – *Hyattidina canalis*; 12 – *Howellella elegans*; 13 – *Dayia navicula*; 14 – other brachiopods; 15 – sample numbers; 16 – rarefaction index for number of species at 50-individual sample size.

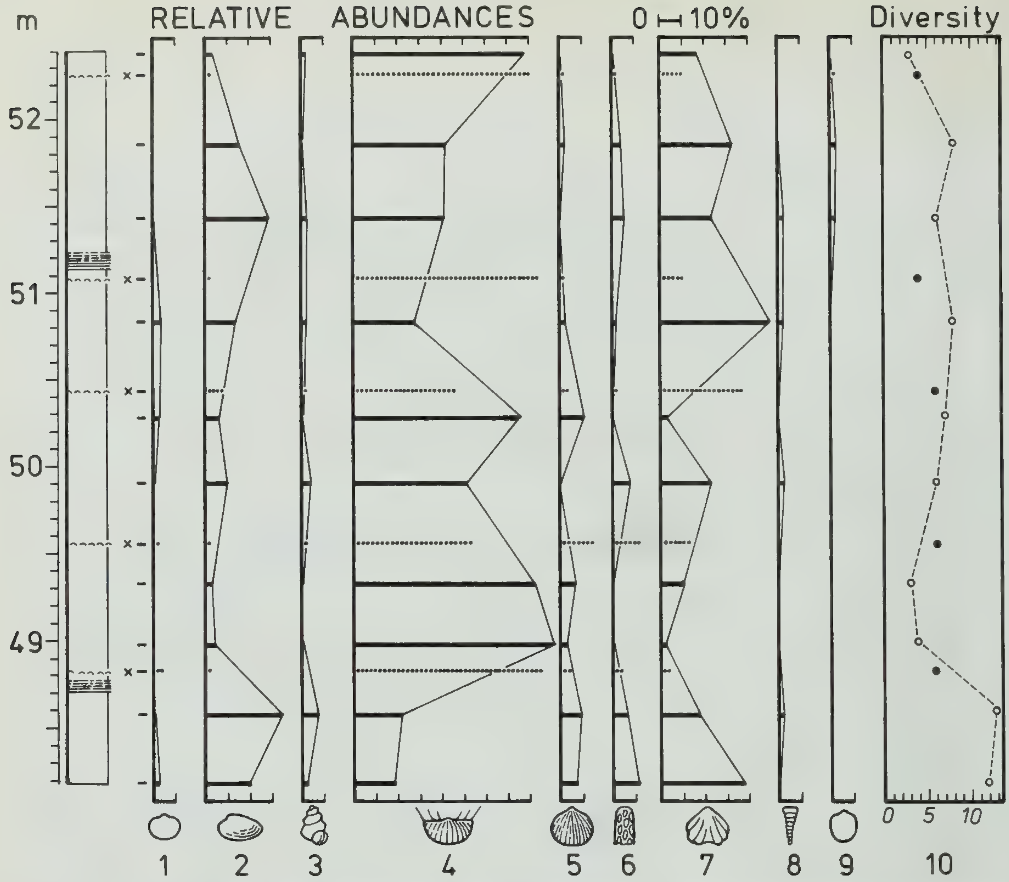


Fig. 11 Faunal comparison of transported assemblages (dotted bars) and disturbed neighbourhood assemblages (solid bars) in the *Protochonetes ludloviensis* Association, Whitcliffe Beds, section 4A, Ledbury, based on mean count of 89 individuals per sample. 1 – various brachiopods; 2 – bivalves; 3 – gastropods; 4 – *Protochonetes ludloviensis*; 6 – bryozoa; 7 – '*Camarotoechia*' *nucula*; 8 – *Cornulites serpularius* and *Serpulites longissimus*; 9 – *Dayia navicula*; 10 – rarefaction index for number of species at 50-individual sample size (solid circles = transported assemblages).

grounds, as explained in the two previous sections. Based on this, the faunal characteristics of transported assemblages are empirically described and compared with the fauna of disturbed neighbourhood assemblages. This establishes some relative effects of shell transport among Ludlow shelf faunas of the study area.

Comparisons between the two types of assemblage were made with a simple 2 × 2 contingency test (for example, number of bivalves versus number of brachiopods in transported assemblages and disturbed neighbourhood assemblages). Data and χ^2 values are given in Tables 6–12.

Articulation of brachiopods

Brachiopods with resorbtion in the tooth-socket structure show locally high rates of articulation in all sedimentary facies, with up to 60% of specimens occurring as whole shells in some samples. For brachiopods without resorbtion in the tooth-socket structure, a maximum of 20% articulated specimens occurs in the mudstone facies. Articulation of these types of brachiopods significantly decreases from the mudstone facies to the bioturbated siltstone facies and coquinoid siltstone facies, which may result from more agitated conditions of sediment deposition. This relation is shown for *Isorthis* and *Howellella* in Table 6.

Table 6 Articulation data for two deltidiodont brachiopods; note the continuous stratigraphic trends. c – coquinoid siltstone facies; b – bioturbated siltstone facies; m – mudstone facies; upSw – upper phase of *S. wilsoni* Association; lpSw – lower phase of *S. wilsoni* Association; Ml – *M. laevigata* Association; Go – *G. obovata* Association; LLB – Lower Leintwardine Beds; LBB – Lower Bringewood Beds; MEB – Middle Elton Beds

facies	association	whole shells	separate valves	per cent articulated	stratigraphic unit
Isorthis clivosa and *I. orbicularis*					
c	upSw	11	372	2·9	LLB
b	lpSw	13	270	4·6	LBB
b	Ml	89	1349	6·2	LBB
m	Go	483	2043	23·7	MEB
Howellella elegans					
c	upSw	3	304	1·0	LLB
b	Ml	18	518	3·4	LBB
m	Go	34	216	13·6	MEB

Table 7 Comparison of articulation between disturbed neighbourhood assemblages and transported assemblages for selected brachiopods. Pl – *P. ludloviensis* Association; upSw – upper phase of *S. wilsoni* Association; lpSw – lower phase of *S. wilsoni* Association

association	assemblage type	whole shells	separate valves	χ^2	significant difference?
Isorthis orbicularis					
upSw	disturbed neighbourhood	11	372	1·4	no
	transported	3	216		
lpSw	disturbed neighbourhood	13	270	0·7	no
	transported	3	105		
Salopina lunata					
Pl	disturbed neighbourhood	41	486	11	yes
	transported	26	713		
upSw	disturbed neighbourhood	7	190	6	yes
	transported	3	398		
Howellella elegans					
upSw	disturbed neighbourhood	3	304	2·5	no
	transported	1	521		
lpSw	disturbed neighbourhood	11	867	1·6	no
	transported	5	773		
'*Camarotoechia*' *nucula*					
Pl	disturbed neighbourhood	386	1088	18	yes
	transported	94	451		
upSw	disturbed neighbourhood	118	716	24	yes
	transported	42	622		

Comparison of brachiopod articulation between disturbed neighbourhood and transported assemblages indicates that transport on the Ludlow shelf related variably to further disarticulation of shells. Within transported assemblages, there is a significant reduction in articulated shells of *Salopina* and '*Camarotoechia*' (Table 7). However, no significant difference in articulation of *Isorthis* and *Howellella* is shown between transported and disturbed neighbourhood assemblages (Table 7).

Valve sorting of brachiopods

There is a preponderance of pedicle valves in Orthida, Strophomenida, Pentamerida and some Spiriferida in all Ludlow shelf facies. This is a very general phenomenon among Silurian faunas, and has also been noted by Ziegler *et al.* (1968*a*). The scale of this relation cannot be explained by local sedimentary sorting, and must involve greater susceptibility of brachial valves to mechanical and biological destruction.

In Ludlow sediments, sorting of valves in disturbed neighbourhood assemblages will be considered as the original sample drawn upon to produce valve ratios in transported assemblages. Differences between the two assemblage types can be assigned to the effects of any additional sorting during transport. Data in Table 8 show that transport may or may not involve valve sorting relative to valve ratios encountered in disturbed neighbourhood assemblages. Where further sorting occurs, it usually involves increased abundance of brachial valves in transported assemblages. Transported *Isorthis*, *Salopina* and *Protochonetes* show a closer approach to unity of the ratio of number of pedicle to brachial valves than in disturbed neighbourhood assemblages

Table 8 Comparison of valve sorting between disturbed neighbourhood assemblages and transported assemblages for selected brachiopods. Designations for associations as in Table 7

association	assemblage type	pedicle valves	brachial valves	χ^2	significant difference?
Isorthis orbicularis					
upSw	disturbed neighbourhood	223	149	30	yes
	transported	79	137		
lpSw	disturbed neighbourhood	175	95	9	yes
	transported	50	55		
Salopina lunata					
Pl	disturbed neighbourhood	277	209	0·2	no
	transported	396	317		
upSw	disturbed neighbourhood	131	59	15	yes
	transported	208	190		
Protochonetes ludloviensis					
Pl	disturbed neighbourhood	1772	454	0·06	no
	transported	1426	358		
upSw	disturbed neighbourhood	174	37	8	yes
	transported	216	86		
'*Camarotoechia*' *nucula*					
Pl	disturbed neighbourhood	432	488	0·1	no
	transported	187	212		
upSw	disturbed neighbourhood	198	308	1·6	no
	transported	196	258		

(Table 8). Rapid transport and permanent burial of brachial valves of these taxa possibly protected them from forms of mechanical or biological destruction operative in disturbed neighbourhood assemblages.

Breakage of brachiopod shells

Within disturbed neighbourhood assemblages, 10% of brachiopod shells and valves show primary non-compactional breakage in the mudstone facies, 21% are broken in the bioturbated siltstone facies and 5% are broken in the coquinoid siltstone facies. These differences are highly significant (Table 9). Greatest proportion of breakage in the two distal shelf, low-energy facies suggests long-term exposure of the shells at the sediment surface, and their continued disturbance by burrowers. In the coquinoid siltstone facies, shells were probably buried more rapidly and permanently, and protected from a great amount of breakage. Broken edges of shells in all facies are unabraded, and surface ornament is also sharply preserved.

Table 9 Primary, non-compactional shell breakage in Ludlow brachiopods. c – coquinoid siltstone facies; b – bioturbated siltstone facies; m – mudstone facies; Pl – *P. ludloviensis* Association; Sw – *S. wilsoni* Association; Ml – *M. laevigata* Association; Go – *G. obovata* Association

facies	association	section	assemblage type	broken shells	whole shells	χ^2	significant difference?
c	Pl	2B, 2C	disturbed neighbourhood	40	674	85	yes
b	Sw, Ml	3A	disturbed neighbourhood	296	1109		
c	Pl	2B, 2C	disturbed neighbourhood	40	674	12	yes
m	Go	5I	disturbed neighbourhood	252	2338		
c	Pl	2B, 2C	disturbed neighbourhood	40	674	0·4	no
c	Pl	2B, 2C	transported	34	671		
c	Pl	5B, 5C	disturbed neighbourhood	19	352	0·8	no
c	Pl	5A	transported	9	239		
b	Sw, Ml	3A	disturbed neighbourhood	296	1109	23	yes
b	Sw, Ml	3A	transported	94	655		

In the bioturbated siltstone facies, transported assemblages contain a significantly lower proportion of broken shells than do disturbed neighbourhood assemblages (Table 9). There is no significant difference in shell breakage proportion between the two assemblage types in the coquinoid siltstone facies (Table 9). Transport of shells on the Ludlow shelf does not appear to have contributed to shell breakage, probably because it was of a turbidity current type, as discussed later. This emphasizes that the shell breakage which does occur is probably a result of prolonged exposure under low-energy conditions.

Infauna – epifauna relations

Of 104 *Lingula* collected from the bioturbated siltstone facies and coquinoid siltstone facies, only one specimen has been found in a transported shell bed assemblage. The same relation is shown by bivalves, which were probably all infaunal or semi-infaunal, except for *Palaeopecten danbyi*. Table 10 shows the proportions of infaunal bivalves to epifaunal brachiopods in several communities from the two facies. Bivalves are significantly concentrated in disturbed neighbourhood assemblages, and are very poorly represented in transported assemblages. This relation is also shown in stratigraphic diagrams in Figs 10–11, pp. 201–2. It indicates that storm events on the Ludlow shelf carried and concentrated epifauna, while leaving infauna relatively unaffected. Another taphonomic consequence of this phenomenon is lower species diversity of transported assemblages relative to disturbed neighbourhood assemblages (Fig. 11).

Table 10 Comparative abundance of articulate brachiopods and bivalves between disturbed neighbourhood assemblages and transported assemblages. χ^2 tests between assemblage types within each association show a significant concentration of bivalves in disturbed neighbourhood assemblages. Pl – *P. ludloviensis* Association; So – *S. ornatella* Association; upSw – upper phase of *S. wilsoni* Association; lpSw – lower phase of *S. wilsoni* Association

association	assemblage type	articulate brachiopod individuals	bivalve individuals	bivalves as % of total
Pl	disturbed neighbourhood	3250	408	11·1
Pl	transported	2254	41	1·8
So	disturbed neighbourhood	694	68	8·9
So	transported	434	11	2·5
upSw	disturbed neighbourhood	1779	104	5·5
upSw	transported	2463	44	1·7
lpSw	disturbed neighbourhood	2281	63	2·7
lpSw	transported	1011	9	0·9

Life habit groups of brachiopods

Different life habit groups of brachiopods appear to show variable susceptibility to transport. Three major groups are considered in the following discussion.

1. Pedically-attached brachiopods, which include all forms not included in the following two groups.
2. Strophomenida, which were mainly unattached.
3. Reclining brachiopods, which lived with the beaks inclined into the sediment and the commissure oriented upwards. Pedicle attachment was weak or absent, and posterior weighting of the shell held individuals in place.

Table 11 Comparative abundance of reclining and pedunculate brachiopods (as defined in text) between disturbed neighbourhood and transported assemblages. c – coquinoid siltstone facies; b – bioturbated siltstone facies; So – *S. ornatella* Association; upSw – upper phase of *S. wilsoni* Association; lpSw – lower phase of *S. wilsoni* Association; Ml – *M. laevigata* Association

facies	association	assemblage type	reclining	pedunculate	χ^2	significant difference?
c	So	disturbed neighbourhood	161	327	17	yes
		transported	23	126		
c	upSw	disturbed neighbourhood	350	1214	244	yes
		transported	1041	1161		
b	lpSw	disturbed neighbourhood	972	1062	109	yes
		transported	276	716		
b	Ml	disturbed neighbourhood	149	76	1·2	no
		transported	90	58		

Data comparing pedunculate and reclining brachiopods are given in Table 11. In the coquinoid siltstone facies, reclining forms are dominated by *Sphaerirhynchia*, *Hyattidina* and *Dayia*, and are significantly concentrated in transported assemblages. No significant concentration, however, is apparent in the bioturbated siltstone facies. Comparisons of pedunculate brachiopods and Strophomenida show no difference in distribution in the bioturbated siltstone facies, but a significant concentration of Strophomenida in transported assemblages of the coquinoid siltstone facies (Table 12). These results might reflect lack of attachment and easier susceptibility to movement of reclining brachiopods and Strophomenida.

Table 12 Comparative abundance of strophomenide and pedunculate brachiopods between disturbed neighbourhood assemblages and transported assemblages. c – coquinoid siltstone facies; b – bioturbated siltstone facies; Pl – *P. ludloviensis* Association; So – *S. ornatella* Association; upSw – upper phase of *S. wilsoni* Association; lpSw – lower phase of *S. wilsoni* Association; Ml – *M. laevigata* Association

facies	association	assemblage type	strophomenide	pedunculate	χ^2	significant difference ?
c	Pl	disturbed neighbourhood	1813	1420	31	yes
		transported	1431	821		
c	So	disturbed neighbourhood	306	327	44	yes
		transported	285	126		
c	upSw	disturbed neighbourhood	210	1214	7	yes
		transported	265	1161		
b	lpSw	disturbed neighbourhood	247	1062	111	yes
		transported	19	716		
b	Ml	disturbed neighbourhood	168	76	1·5	no
		transported	163	58		

Community integrity of transported assemblages

The stratigraphic profiles of fauna constructed in this study clearly indicate that transported shell beds in Ludlow sediments contain the same communities as adjacent disturbed neighbourhood assemblages, apart from the relations discussed above. The sequence from the bioturbated siltstone facies to coquinoid siltstone facies (Lower Bringewood Beds to Whitcliffe Beds) contains six benthic communities in ascending stratigraphic order, as shown in Fig. 12. Within the stratigraphic interval of occurrence in each of these six communities there are beds of transported shells, but in no observed case do these beds include an ecologically mixed or disjunct fauna. The basic community integrity of transported assemblages can be seen in the faunal profiles shown in Figs 16–20 (pp. 213–8), where such samples are indicated with an ' × '.

Summary and general implications of shell transport

Comparison of disturbed neighbourhood and transported assemblages in Ludlow shelf sediments produces the following conclusions regarding the effect of shell transport.

1. Minor contribution to disarticulation and concentration of brachial valves in some brachiopods.
2. No effect in shell breakage.
3. Concentration of epifauna, with very little effect upon infauna.
4. Selective removal and concentration of certain strophomenides and reclining brachiopods in the coquinoid siltstone facies.
5. No mixing of benthic community elements.

According to the storm-related model of shelf sedimentation presented in the sedimentology section, most transport of Ludlow shells occurred in association with very rapid turbidity currents. During storms, shells were probably incorporated and partially suspended in rapidly-moving 'clouds' of suspended silt, finally settling as coarse basal layers with reduction of the current strength. This form of transport would explain the lack of infauna, concentration of epifauna and lack of abrasion and shell breakage in transported assemblages. It could result in the movement of shells for kilometres across the shelf without mechanical damage. Reineck & Singh (1973) have noted the long-range transport of living *Hydrobia* in North Sea storm sedimentation.

Nevertheless, shell transport during Ludlow storm sedimentation did not mix different communities. Although differing in quantitative details, transported assemblages are similar in content of epifaunal species to adjacent disturbed neighbourhood assemblages. When an ecological change from one community to another occurs in bioturbated parts of a stratigraphic section, there is a corresponding change in transported faunas, indicating a contemporaneous change in the *source* of transported shells.

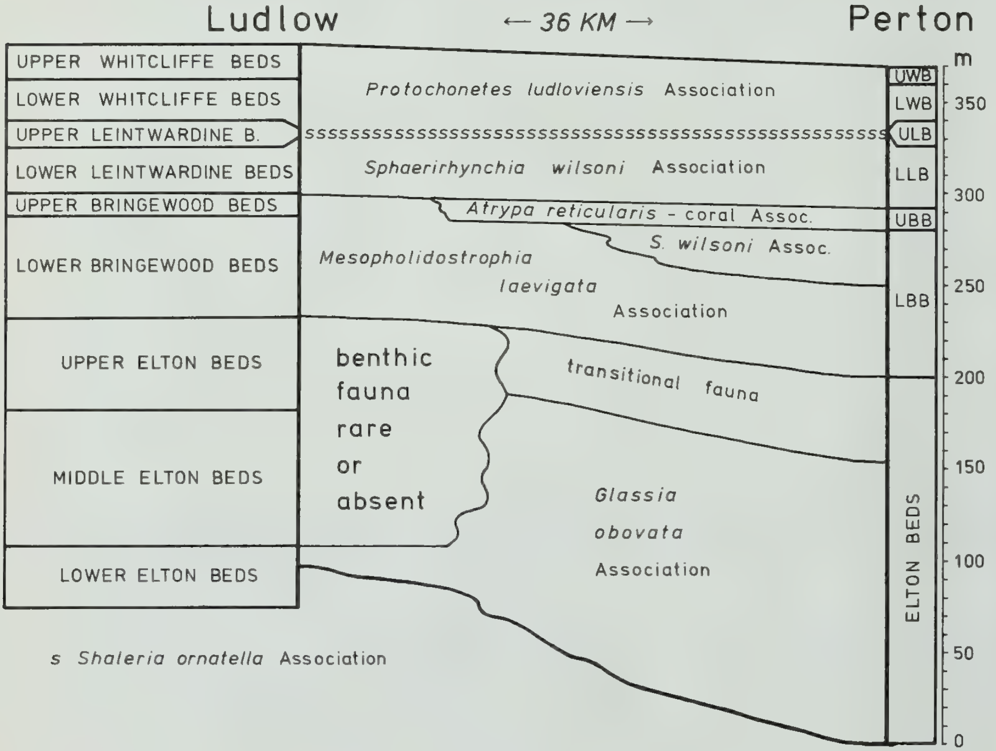

Ludlow
← 36 KM →
Perton
UPPER WHITCLIFFE BEDS
LOWER WHITCLIFFE BEDS
UPPER LEINTWARDINE B.
LOWER LEINTWARDINE BEDS
UPPER BRINGEWOOD BEDS
LOWER BRINGEWOOD BEDS
UPPER ELTON BEDS
MIDDLE ELTON BEDS
LOWER ELTON BEDS
Protochonetes ludloviensis Association
Sphaerirhynchia wilsoni Association
Atrypa reticularis - coral Assoc.
S. wilsoni Assoc.
Mesopholidostrophia laevigata Association
benthic fauna rare or absent
transitional fauna
Glassia obovata Association
s Shaleria ornatella Association
UWB
LWB
ULB
LLB
UBB
LBB
ELTON BEDS
m
350
300
250
200
150
100
50
0

Fig. 12 Generalized cross-section showing stratigraphic relations of benthic communities described in text.

One explanation is that shell transport may have occurred over a distance of only metres or less. This is possible on the distal fringe of a mass-deposited sheet of silt, or in the case of swell lags discussed earlier, but it is not a suitable general explanation for the abundant shell beds in the Ludlow sections. Another possibility is that the Ludlow communities of the Welsh Borderland synchronously occupied such wide expanses of shelf that transport over distances of kilometres would not introduce mixed or disjunct faunas into the areas studied. This explanation is supported by the correlations of Holland *et al.* (1963) and the discussion given in the stratigraphy section.

Community definition

The transect method of community definition

A descriptive recognition of past associations of organisms must precede their biological or dynamic interpretation. For this purpose, the community definition of Ehrlich *et al.* (1973) will be used. 'The organisms existing at a particular place and time may be called a *community*. The word has no special biological meaning, it is merely a useful descriptive term.' Petersen (1918) showed that particular combinations of benthos occupy discrete areas of seafloor, and can be mapped. One can thus define a community by specifying either faunal composition or areal boundaries interchangeably.

Jurgen Dörjes has applied a transect method to the areal definition of modern marine benthic communities (Dörjes *et al.* 1969, 1970; Dörjes 1971, 1972). An example of this work is reproduced in Fig. 13. Samples are taken along a line across a known environmental gradient, usually perpendicular to a coastline and boundaries of sedimentary facies. The transect line is drawn on paper, and occurrences of species are plotted along it according to sample to produce a graphic profile of faunal distribution. The profiles are then divided into contiguous segments which define communities, according to distinctive overlaps of species ranges along the line of transect (Fig. 13).

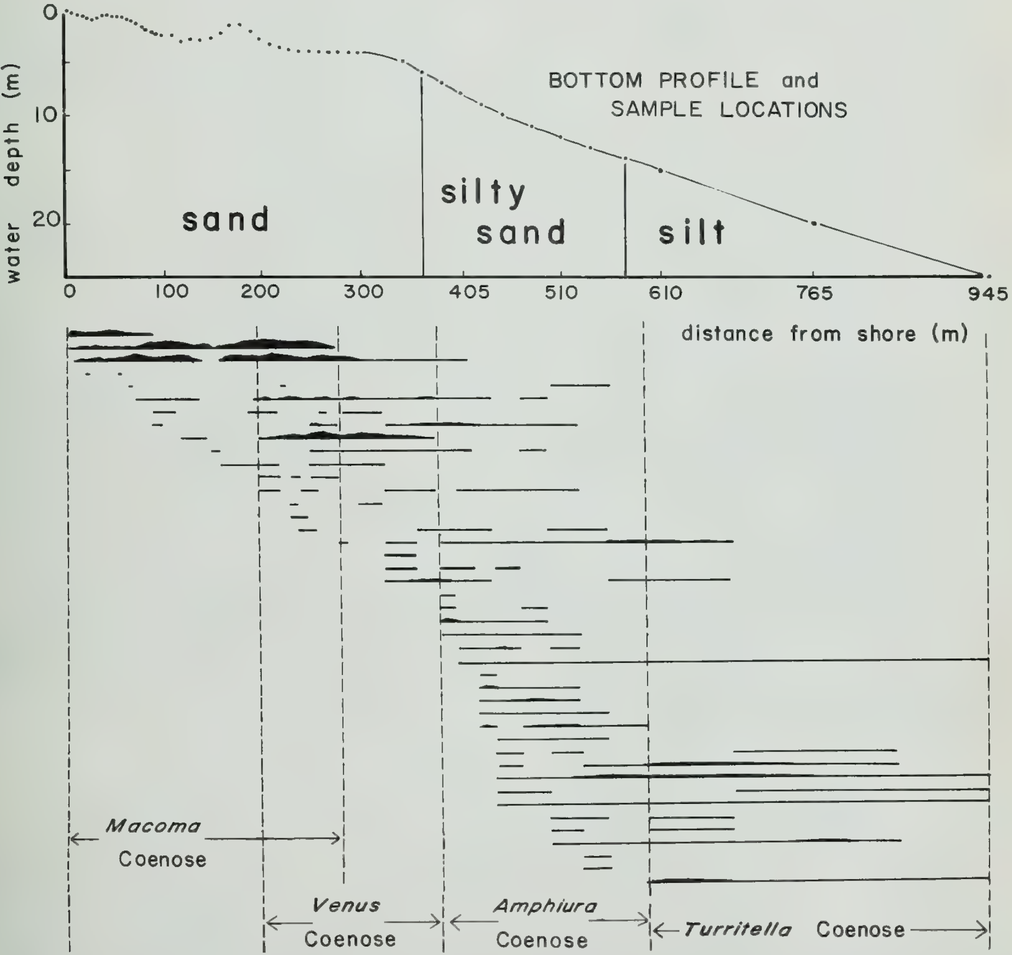


Fig. 13 Distribution of mollusc species along a sedimentary-bathymetric gradient in the Gulf of Gaeta, Italy, illustrating the transect method of defining communities. Modified from Dörjes (1971 : fig. 5).

The transect method provides a direct picture of community boundaries and gradations, and eliminates the need for statistical comparison of scattered samples. Some community boundaries represent very sharp changes in faunal composition, as where sand shoals border mud-filled troughs (Dörjes 1972 : pl. 2). In other transects, the faunas of communities grade into one another along continuous transitions of sediments (Fig. 13). This phenomenon, where community gradations reflect environmental gradients, has also been discussed by Johnson (1972).

Application of the transect method to stratigraphic sections

The transect method for defining benthic communities has been applied to stratigraphic sections in the Welsh Borderland according to the sampling methods described (p. 178). Stratigraphic sections have been treated primarily as an environmental rather than purely a time gradient, following the succession of sedimentary facies described earlier. Faunal distribution along the stratigraphic gradient of environments is used to define benthic communities.

Faunal composition at each sampling point along the measured sections has been plotted according to the relative abundances of individuals of each constituent taxon. Histograms for each taxon, arranged in stratigraphic order, are then joined by lines to form a continuous stratigraphic profile of its abundance. The resulting diagrams, or 'faunal profiles', for measured sections are grouped as in Figs 16–21. Along with the statistics in Appendix 3 (pp. 262–74), they constitute the basic source for community definitions.

Several important points must be noted concerning the faunal profiles in Figs 16–21:

1. A key to symbols in the profiles is given in Figs 14 and 15.
2. Very low relative abundances have been exaggerated to values of 3 or 5% to be visible in the diagrams. The total relative abundances shown for each sample thus often exceed 100%.
3. Samples of fewer than 30 individuals were not plotted, so that the average sampling error for a relative abundance shown is less than 5% (see Appendix 2, p. 260).
4. Most samples are of 50–100 individuals, and the absence of any given species from a sample may be an artefact of insufficient sampling (Appendix 2). However, the continued absence of a species from several samples in stratigraphic succession is evidence for genuine non-occurrence. Representative sample sizes used for the faunal profiles are given in Tables 17–20 in Appendix 3.
5. Profiles of diversity give the number of species at 50-individual sample size, based on both direct count and the rarefaction method of Sanders (1968). In samples with abundant bryozoa, these diversity measurements are conservative, as this group was not given species-level study in thin section.
6. The faunal profiles are compilations from the more complete set of basic data given in Appendix 3. Relative abundances of species other than brachiopods are combined in the faunal profiles according to phylum or class because of low abundances and the sporadic occurrence of most individual species. This has been done as a matter of convenience in constructing the diagrams, and does not indicate that the non-brachiopod groups have been omitted from the community analysis. The species-level data for molluscs, trilobites and minor groups in the Ludlow sections is summarized in Appendix 3.

Definition of the Ludlow shelf communities

Following the transect method, Ludlow communities are defined, spatially, as stratigraphically successive portions of the faunal profiles. Community boundaries were chosen by inspection of the stratigraphic ranges and changes in abundance of taxa, and are designated as dotted lines across the faunal profiles, perpendicular to the stratigraphic column. Several examples of these boundaries can be seen in Figs 16 and 17. In most cases, the nature of a faunal change permits the unequivocal location of an ecological boundary within a 2–5 m stratigraphic interval. The significance of this is discussed later.

The benthic communities recognized here are designated with the formal term 'Association', preceded by the name of one of their species, and the terms 'community' and 'association' are used interchangeably throughout the text. It must be re-emphasized that these 'Associations' are defined on a spatial basis, as the total fauna in a designated stratigraphic interval. They are not defined or intended to be recognized by some specific numerical combination of taxa. A stratigraphic summary of all the associations defined in the measured sections is shown in Fig. 12, p. 208.

Glassia obovata Association

The *Glassia obovata* Association is restricted to the Elton Beds, where it occurs throughout the mudstone facies and in minor bioturbated intervals within the laminated shale facies. Small brachiopods, bivalves and trilobites are the dominant forms, and although species content is relatively constant throughout the areas studied, relative abundances of different groups show significant variations from one section to another. Stratigraphic profiles of this community are given in Figs 19, 21, 22 and 23, and checklists of species are given in Appendix 3, Tables 15 and 17.

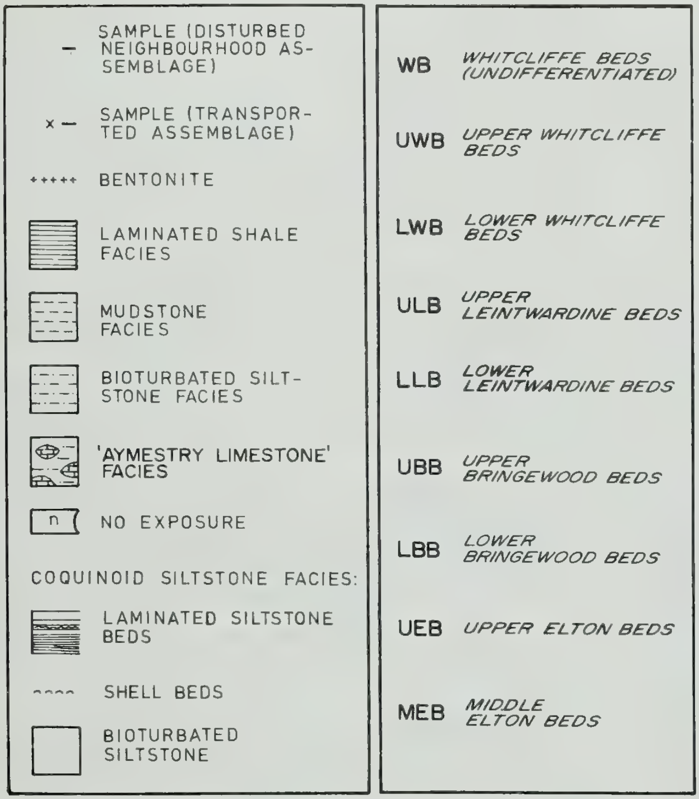

SAMPLE (DISTURBED NEIGHBOURHOOD ASSEMBLAGE)
SAMPLE (TRANSPORTED ASSEMBLAGE)
BENTONITE
LAMINATED SHALE FACIES
MUDSTONE FACIES
BIOTURBATED SILTSTONE FACIES
'AYMESTRY LIMESTONE' FACIES
n
NO EXPOSURE
COQUINOID SILTSTONE FACIES:
LAMINATED SILTSTONE BEDS
SHELL BEDS
BIOTURBATED SILTSTONE
WB WHITCLIFFE BEDS (UNDIFFERENTIATED)
UWB UPPER WHITCLIFFE BEDS
LWB LOWER WHITCLIFFE BEDS
ULB UPPER LEINTWARDINE BEDS
LLB LOWER LEINTWARDINE BEDS
UBB UPPER BRINGEWOOD BEDS
LBB LOWER BRINGEWOOD BEDS
UEB UPPER ELTON BEDS
MEB MIDDLE ELTON BEDS

Fig. 14 Standard symbols used in stratigraphic columns in Figs 16–22.

Brachiopods

The most abundant brachiopod occurring in the *G. obovata* Association is the strophomenide *Aegiria grayi*, which is less than 5 mm in size and reaches local densities of 18 000 shells per square metre. *Aegiria grayi* is listed by sample in Appendix 3, but it is not included in calculations or faunal profiles for this community, as it appears to have possessed an epiplanktic mode of life. The main evidence for this is its presence in laminated mudstones of the shelf edge and basin areas in association with a wholly pelagic fauna of graptolites, small orthoconic nautiloids and praecardiacean bivalves. *Aegiria grayi* also appears in association with a pelagic graptolitic fauna in the Upper Leintwardine Beds, again with a distribution centred in the basin and shelf edge (Holland & Lawson 1963). An epiplanktic mode of life for the related Ordovician genera *Sericoidea* and *Chonetoidea* has been shown by Bergström (1968) and Havlíček (1967).

Thirty other brachiopod species have been recorded from the *G. obovata* Association. These species comprise 85% of individuals in the association, and most are below 15 mm in size. One characteristic pattern of brachiopod occurrence is shown in Fig. 22, p. 220. In this example, a variety of species and adaptive types are present in fairly equitable abundances, with continuous and relatively constant densities of shells in the vertical profile of bioturbated mudstone. Each species shows gradual long-term changes in abundance. These cycles are discussed in detail later, and related to optimal periods of larval recruitment. Although the content of brachiopod species in the association remains relatively constant, the cycles of each species' abundance produce subtle and continuous fluctuations in community composition through time.

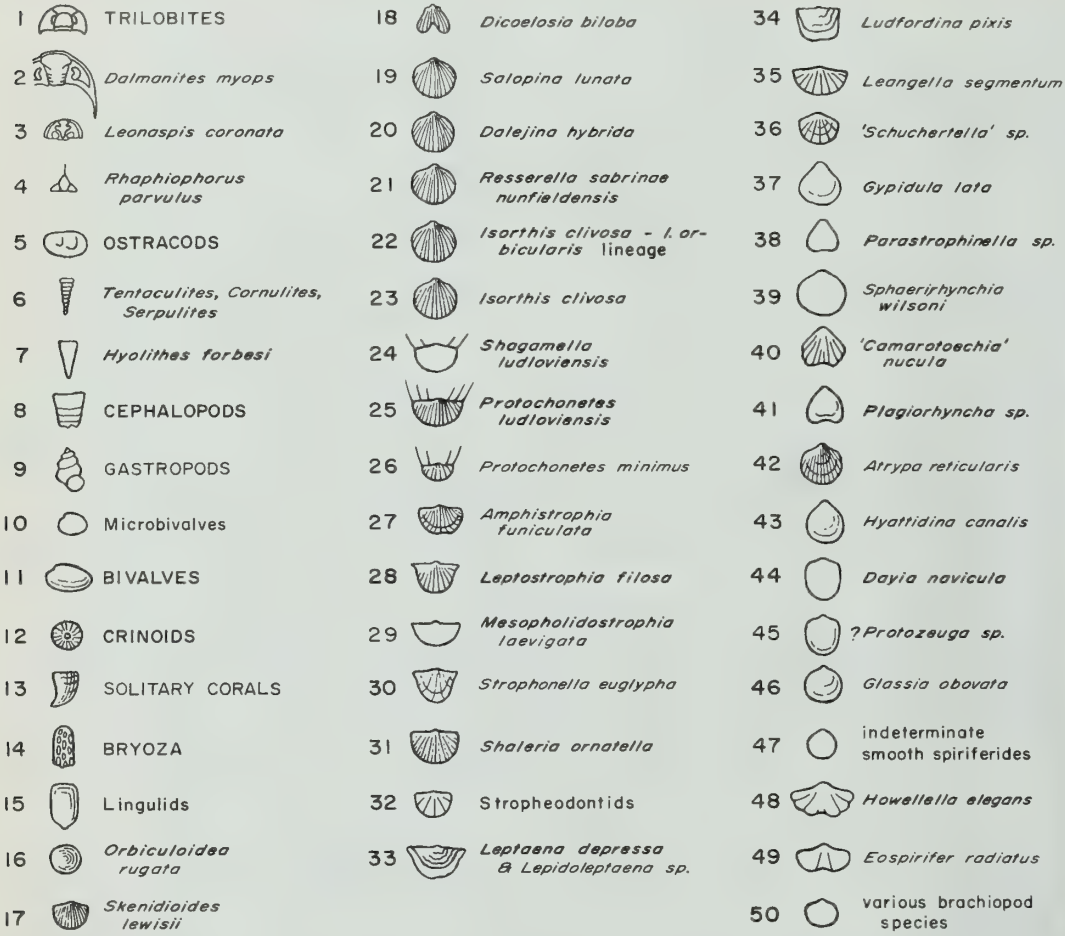

1 TRILOBITES
2 Dalmanites myops
3 Leonaspis coronata
4 Rhaphiophorus parvulus
5 OSTRACODS
6 Tentaculites, Cornulites, Serpulites
7 Hyolithes forbesi
8 CEPHALOPODS
9 GASTROPODS
10 Microbivalves
11 BIVALVES
12 CRINOIDS
13 SOLITARY CORALS
14 BRYOZA
15 Lingulids
16 Orbiculoidea rugata
17 Skenidioides lewisii
18 Dicoelosia biloba
19 Salopina lunata
20 Dalejina hybrida
21 Resserella sabrinae nunfieldensis
22 Isorthis clivosa - I. orbicularis lineage
23 Isorthis clivosa
24 Shagamella ludloviensis
25 Protochonetes ludloviensis
26 Protochonetes minimus
27 Amphistrophia funiculata
28 Leptostrophia filosa
29 Mesopholidostrophia laevigata
30 Strophonella euglypha
31 Shaleria ornatella
32 Stropheodontids
33 Leptaena depressa & Lepidoleptaena sp.
34 Ludfordina pixis
35 Leangella segmentum
36 'Schuchertella' sp.
37 Gypidula lata
38 Parastrophinella sp.
39 Sphaerirhynchia wilsoni
40 'Camarotoechia' nucula
41 Plagiorhyncha sp.
42 Atrypa reticularis
43 Hyattidina canalis
44 Dayia navicula
45 ?Protozeuga sp.
46 Glassia obovata
47 indeterminate smooth spiriferides
48 Howellella elegans
49 Eospirifer radiatus
50 various brachiopod species

Fig. 15 Standard symbols used for species and other taxa in Figs 16–23, 25.

Another pattern of brachiopod occurrence is seen near Perton (Fig. 21, p. 219), where *Isorthis clivosa* and *Glassia obovata* greatly predominate over other brachiopods, and comprise most individuals in the association as a whole. In *Isorthis clivosa*, these fluctuations range through abundances of about 20–80% of the entire shelled fauna, and occur as predictable cycles occupying stratigraphic intervals of 3–7 m. *Glassia obovata* shows a much more erratic stratigraphic pattern, and dense concentrations of articulated individuals come and go suddenly within the vertical profile of bioturbated mudstone (Fig. 21). Species diversity is low where these two forms predominate, and other brachiopods occur sporadically and seldom exceed 10% of individuals per sample.

Parastrophinella sp. is a small plicate pentameracean which plays a minor role in the brachiopod occurrences discussed above. In the laminated shale facies, however, it becomes the most abundant brachiopod of the association (Fig. 23, p. 221). Relatively few brachiopod species of the *G. obovata* Association extend from the mudstone facies to the laminated shale facies.

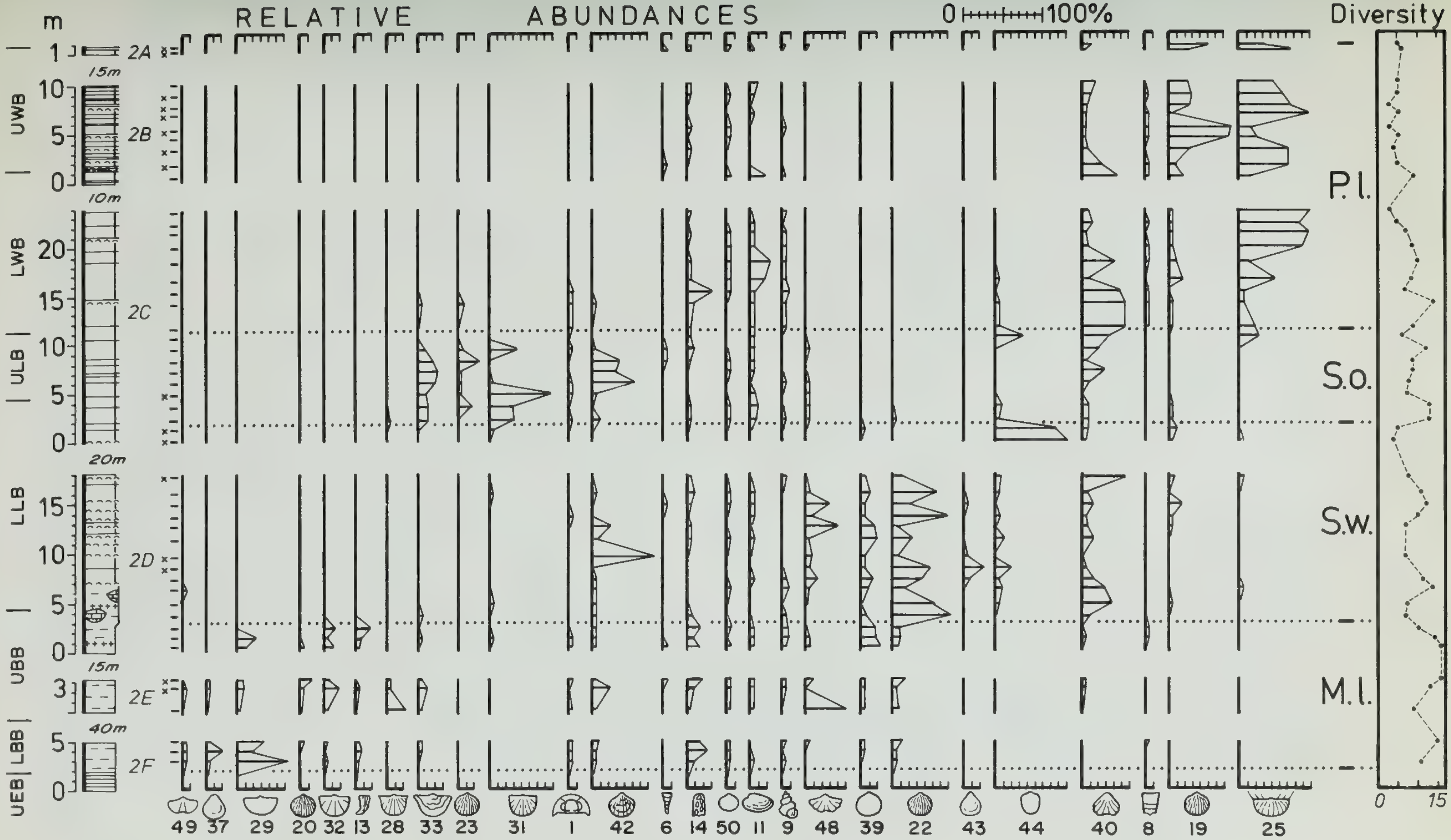


Fig. 16 Faunal profile of the *Protochonetes ludloviensis* Association (Pl), *Shaleria ornatella* Association (So), *Sphaerirhynchia wilsoni* Association (Sw) and *Mesopholidostrophia laevigata* Association (Ml) in the Ludlow area. All sections except 2E contain the type stratigraphic boundaries designated by Holland *et al.* (1963). Symbols are explained in Figs 14 and 15. The diversity scale gives the rarefaction index for number of species at 50-individual sample size.

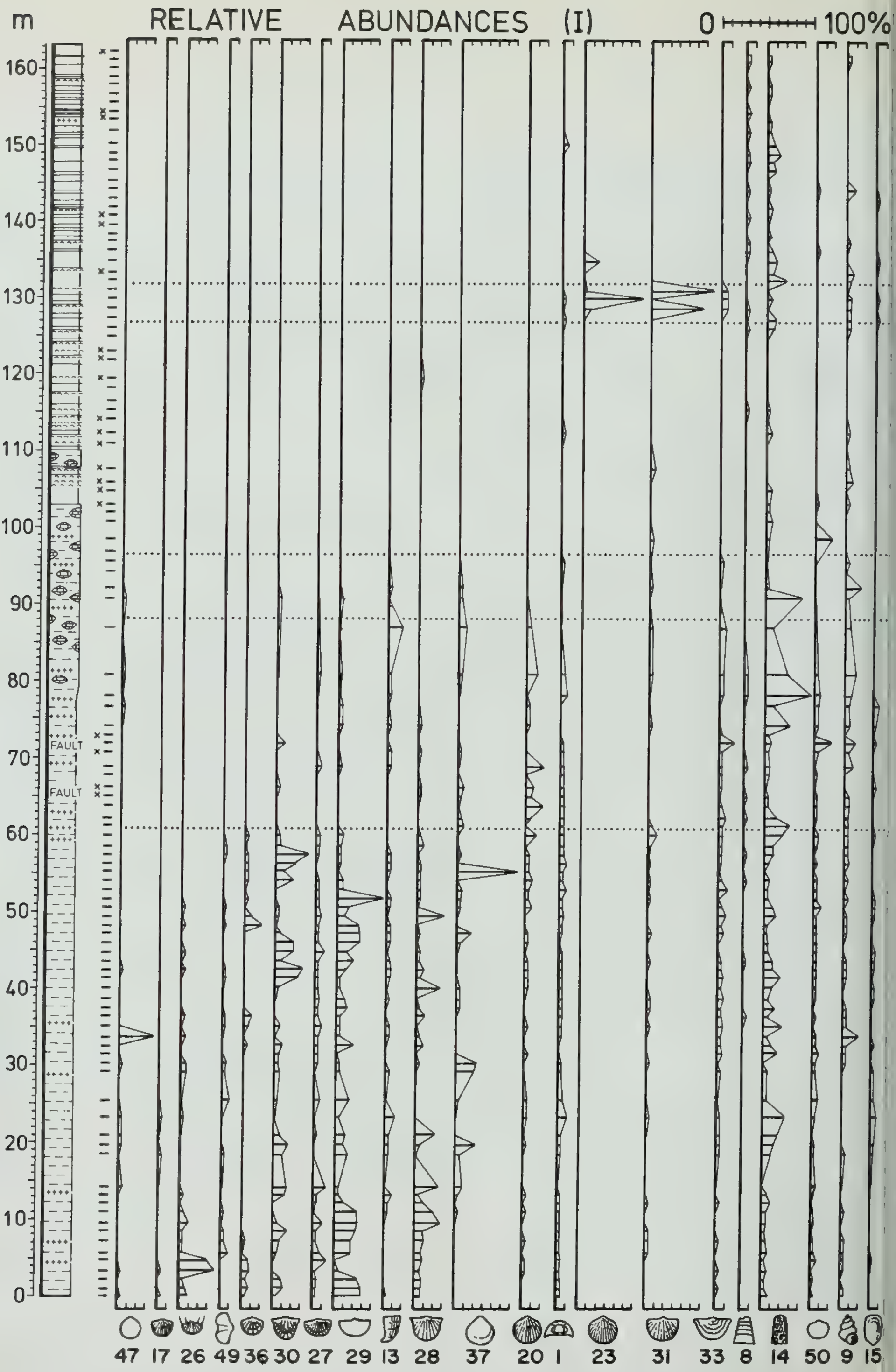
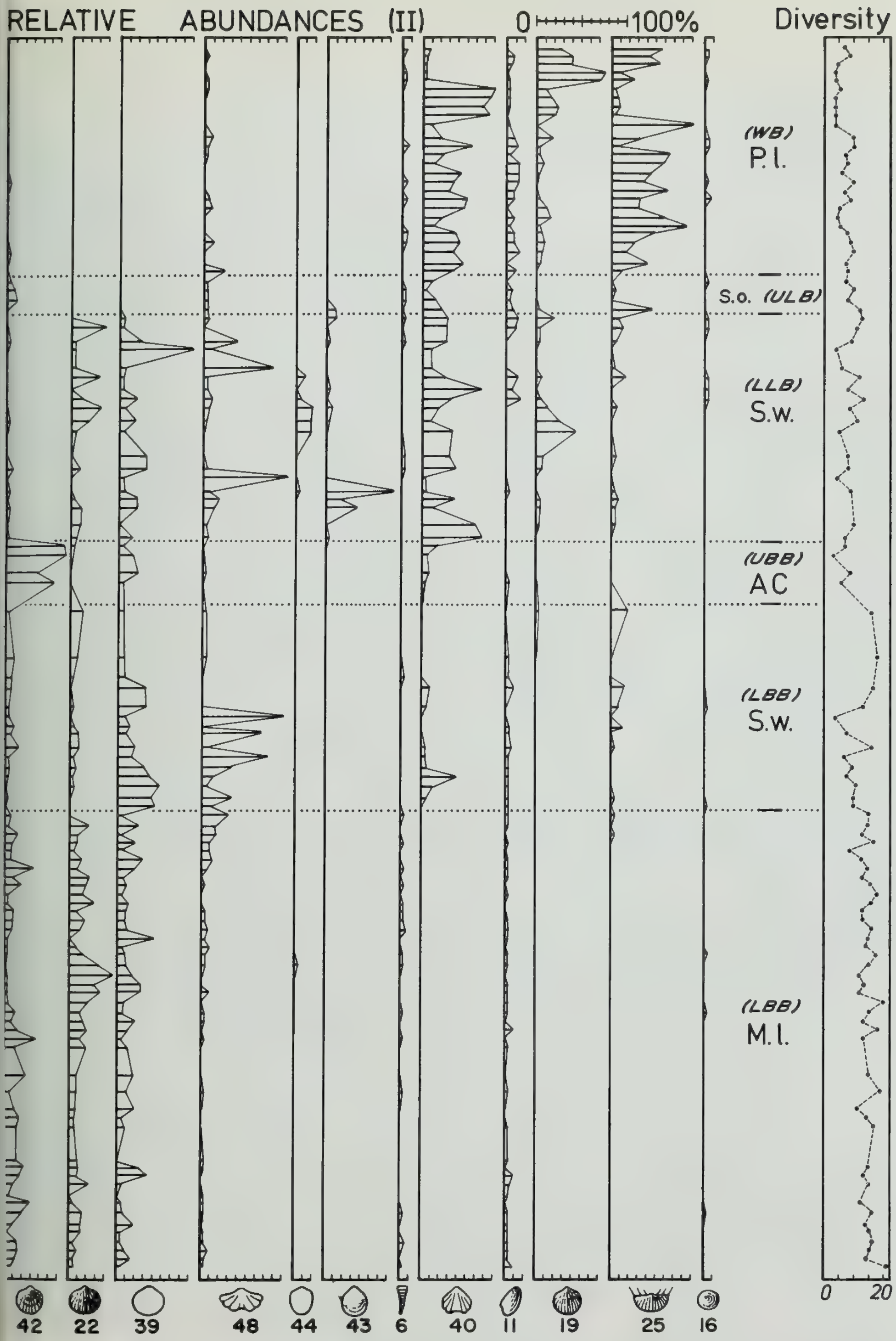


Fig. 17 Faunal profile of the *Protochonetes ludloviensis* Association (Pl), *Shaleria ornatella* Association (So), *laevigata* Association (Ml) in section 3A, Woodbury Quarry. Symbols are explained in Figs 14 and



phaerirhynchia wilsoni Association (Sw), *Atrypa reticularis* – coral Association (AC), and *Mesopholidostrophia*
5. The diversity scale gives the rarefaction index for number of species at 50-individual sample size.

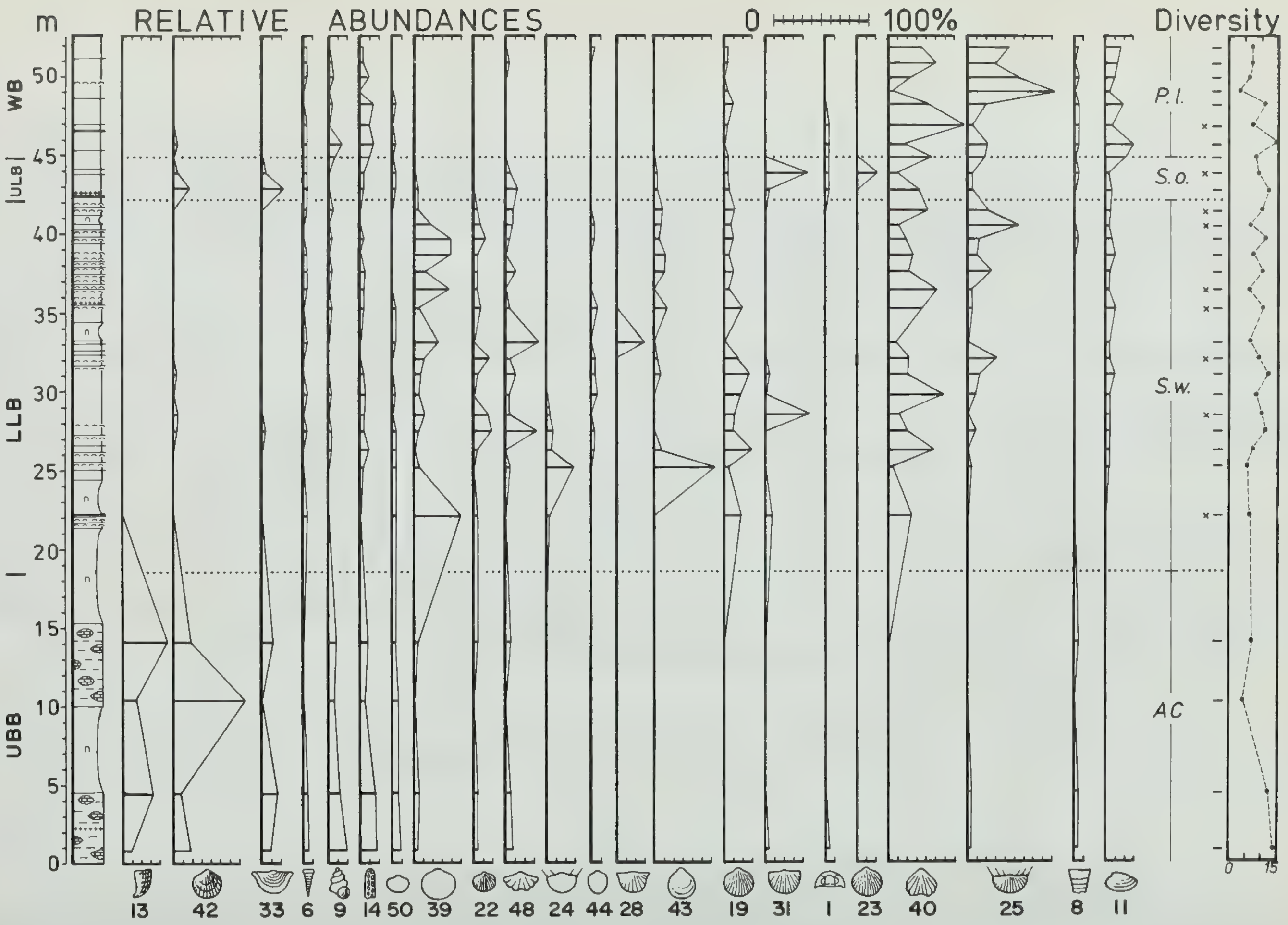


Fig. 18 Faunal profile of the *Protochonetes ludloviensis* Association (Pl), *Shaleria ornatella* Association (So), *Sphaerirhynchia wilsoni* Association (Sw) and *Atrypa reticularis* – coral Association (AC) in section 4A, near Ledbury. Symbols are explained in Figs 14 and 15. The diversity scale gives the rarefaction index for number of species at 50-individual sample size. For more detailed sampling between 35–36 m within this section, see Figs 10 and 11.

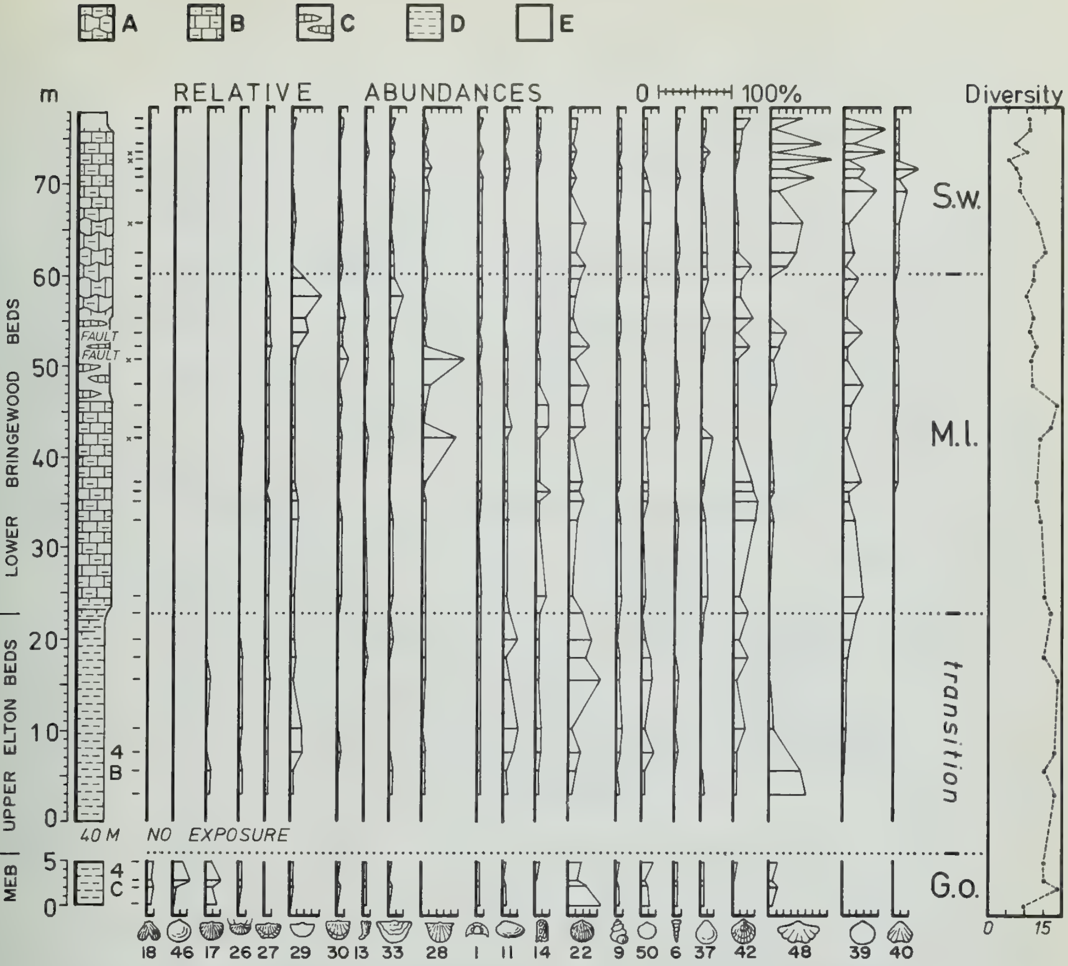


Fig. 19 Faunal profile of the *Sphaerirhynchia wilsoni* Association (Sw), *Mesopholidostrophia laevigata* Association (Ml), transition fauna and *Glassia obovata* Association (Go) in sections 4B and 4C, Ledbury. The diversity scale gives the rarefaction index for number of species at 50-individual sample size. A – massive calcisiltite and silty limestone; B – bedded calcisiltite and silty limestone with shell layers; C – thinly interbedded calcisiltite and limestone; D – mudstone facies; E – bioturbated siltstone. Faunal symbols are explained in Fig. 15.

Small brachiopods with strongly incurved beaks and a probable unattached reclining mode of life are the most abundant life habit group within the *G. obovata* Association. Examples include *Glassia*, *Parastrophinella*, *Plagiorhyncha* and ?*Protozeuga*. *Isorthis* is the most common pedunculate form, but several other taxa with unrestricted pedicle openings, including *Skenidioides*, *Resserella*, *Dalejina*, *Dicoelosia* and *Howellella* are present. The only common strophomenides of the association, *Protochonetes minimus* and *Ludfordina pixis*, did not have a completely free mode of life, but show adaptation for stabilization by spines and a pedicle respectively. Fifty per cent of brachiopod species in the association are more common members of other Ludlow communities, and may be considered at the extremes of their tolerance ranges in the mudstone facies and laminated shale facies.

Bivalves

Twenty-two species of bivalves have been identified from the *G. obovata* Association. Five of

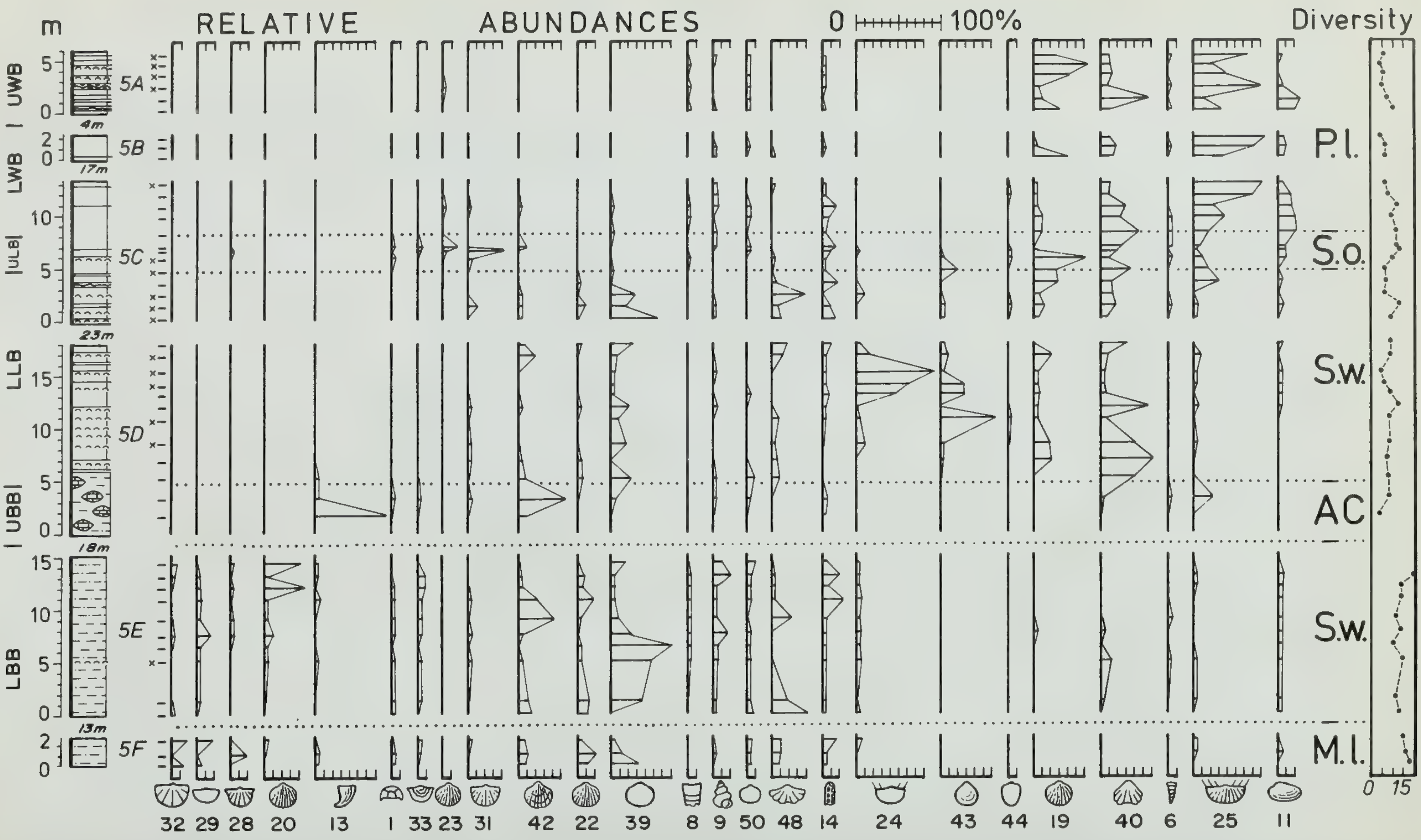


Fig. 20 Faunal profile of the *Protochonetes ludoviensis* Association (Pl), *Shaleria ornatella* Association (So), *Sphaerirhynchia wilsoni* Association (Sw), *Atrypa reticularis* – coral Association (AC), and *Mesopholidostrophia laevigata* Association (Ml) in the Perton area. The diversity scale gives the rarefaction index for number of species at 50-individual sample size. Other symbols are explained in Figs 14 and 15.

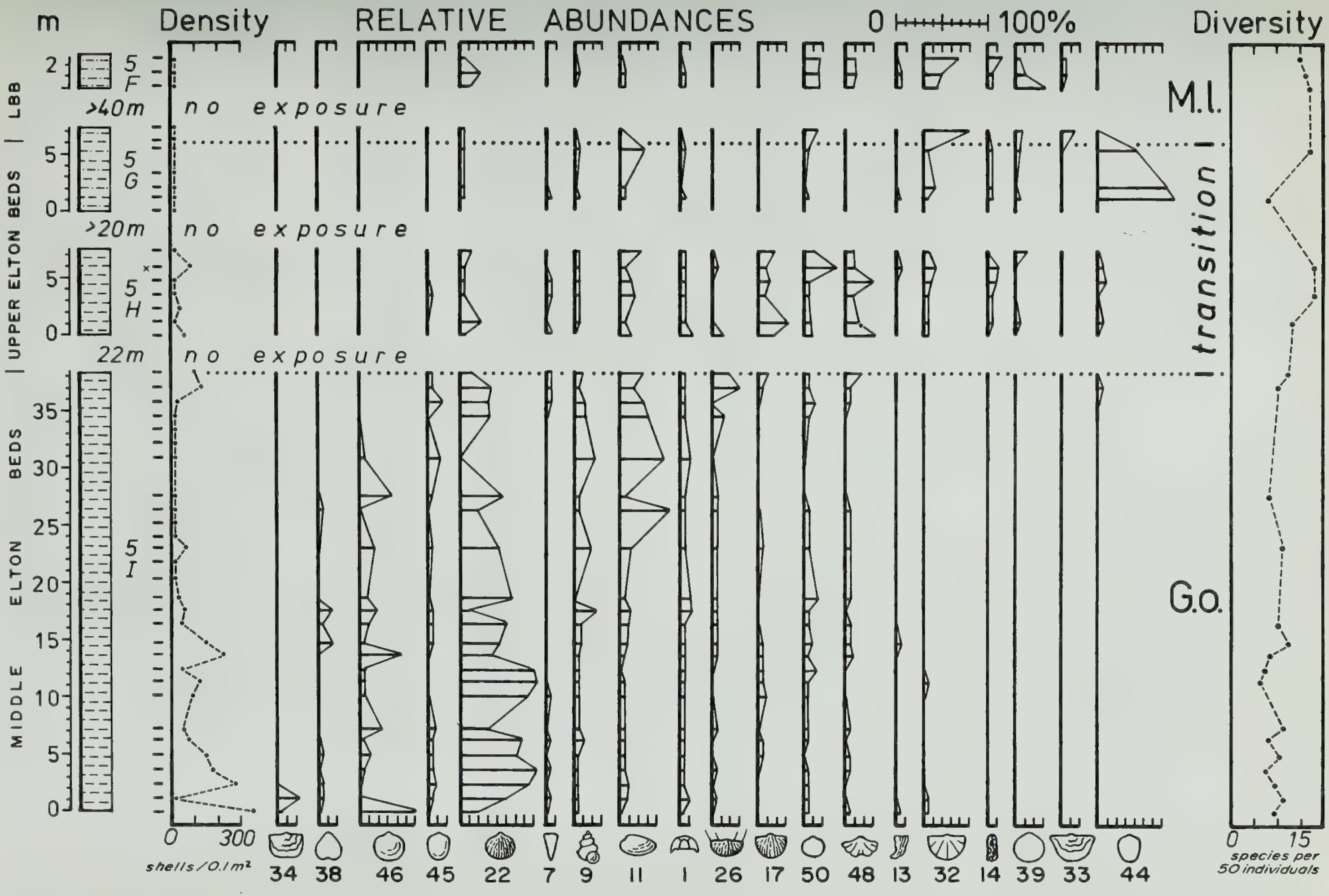


Fig. 21 Faunal profile of the *Mesopholidostrophia laevigata* Association (Ml), transition fauna, and *Glassia obovata* Association (Go) in the Perton area. Four bentonite beds occur in the lower 3 m of section 5I. See Figs 14 and 15 for explanation of symbols.

these species are members of the Praecardiacea, and are mainly restricted to the laminated shale facies. Like *Aegiria*, they have a distribution pattern which corresponds with that of graptolites, and are considered to have had an epiplanktic mode of life. These species are listed in Table 23 of the deposit data; see p. 179.

The free-burrowing nuculoids *Nuculites woolhopensis* and *Praenucula* sp. comprise about half of all bivalve individuals in the *G. obovata* Association. Most shells are below 1 cm in length. These species are commonly found together in samples, and occur throughout profiles of the association in both the mudstone facies and laminated shale facies. In a 10-m portion of bioturbated mudstone in section 5I, *Nuculites* and *Praenucula* become the dominant taxa of the association, reaching combined relative abundances of 40–50% (Fig. 21). This interval corresponds to a decrease in density and relative abundance of brachiopods, and may relate to a decrease in substrate hardness, as discussed later. *Nuculites* and *Praenucula* are also among the most common members of the association in the laminated shale facies (Table 23, deposited). Two other species of small nuculoids, *Nuculites pseudodeltoideus* and *Praectenodonta ludensis*, occur rarely in the mudstone facies.

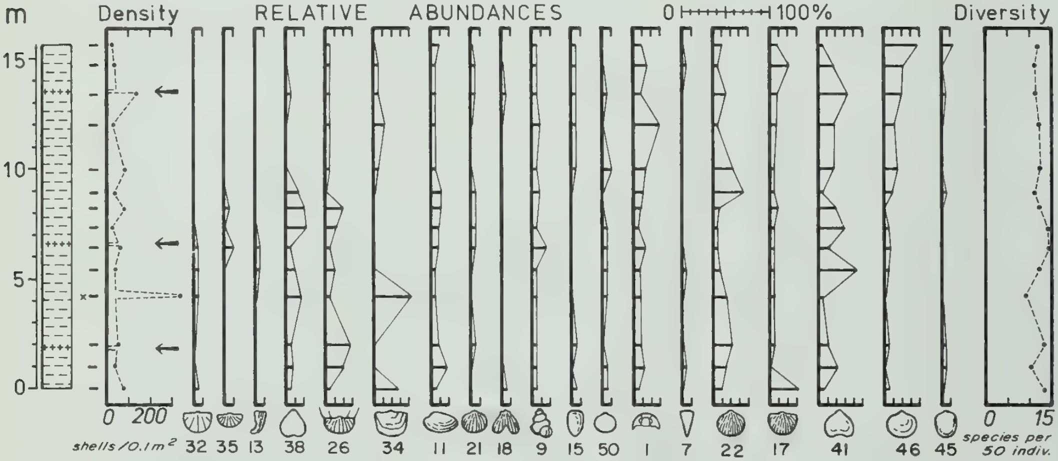


Fig. 22 Faunal profile of the *Glassia obovata* Association in section 1E, Middle Elton Beds, Upper Millichope. Arrows beside the density curve indicate faunal destructions by bentonites. Lithological and faunal symbols are explained in Figs 14 and 15.

Thirteen other bivalve species in the *G. obovata* Association show a very sporadic pattern of occurrence, and are seldom represented by more than one or two individuals per sample. This pattern can be seen in Table 17 (p. 269), and suggests small, widely-separated populations. Most of these species show adaptation for an endobyssate mode of life, but epibyssate and free-burrowing forms are also present.

Gastropods

Gastropods are continuously present throughout stratigraphic profiles of the association, but are seldom represented by more than a few individuals per sample. They are most conspicuous in the laminated shale facies and mudstone intervals dominated by nuculoids, where they reach 10% of the total fauna (Figs 21 and 23). The bellerophontaceans *Cymbularia* and *Sphenosphaera* and the high-spired *Loxonema* and *Sinuspira* predominate among the gastropod fauna, ranging from 5 to 20 mm in size. Ten other gastropod species are listed in Appendix 3.

Cephalopods

'*Orthoceras*' *dimidiatum* and '*O.*' *gregarium* are very common components of the *G. obovata* Association. They have maximum diameters less than 15 mm, no ornament except growth lines

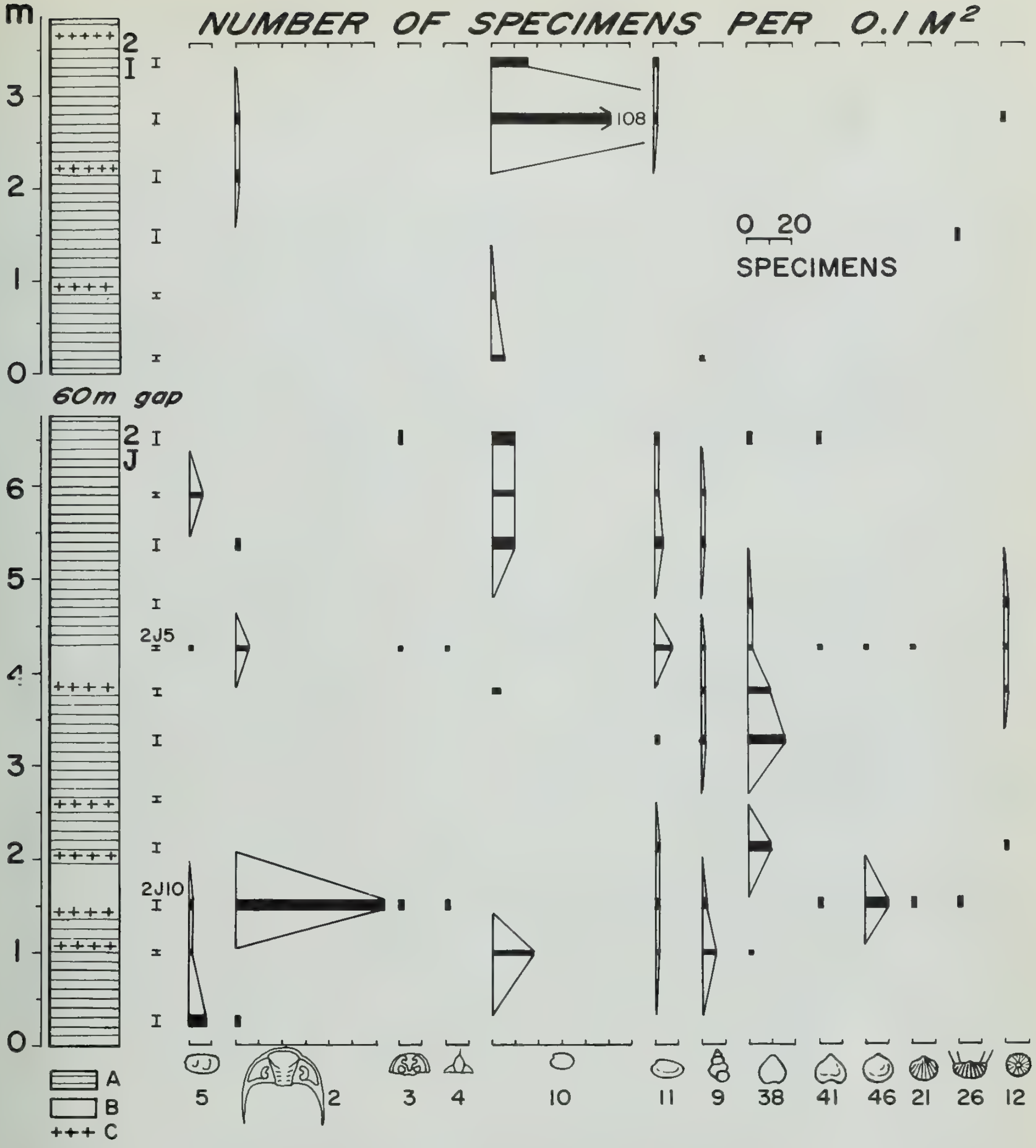


Fig. 23 Densities of benthic invertebrates of the *Glassia obovata* Association in sections 2I and 2J, Middle Elton Beds, Ludlow area. A – laminated shale; B – intensely bioturbated mudstone; C – bentonite. Faunal symbols are explained in Fig. 15.

and a simple orthoconic shell. These cephalopods reach maximum densities in laminated shales of basin and shelf edge areas, in association with graptolites. Like the graptolites, they show a decrease in density from Ludlow eastward across the shelf. This pattern indicates a pelagic mode of life, and lack of direct relation to bottom faunas.

Another group of cephalopods in the Elton Beds contrasts in their strong patterns of ornamentation, somewhat thicker shells, occasional departure from an orthoconic form and preferential association with benthic faunas rather than graptolites. These cephalopods are listed in

Table 15 (pp. 265–6) and include species of *Cyrtocycloceras*, '*Cyrtoceras*', *Dawsonoceras* and *Kionoceras*. They are rare or absent in the laminated shale facies, but occur sporadically throughout the mudstone facies with the *G. obovata* Association, generally in relative abundances of less than 1% of the total fauna. Their distribution suggests a nektobenthic mode of life and an ecological relation to bottom faunas, probably as predators.

Trilobites

Six species of trilobites have been recorded from the *G. obovata* Association, which appears to be their maximum diversity in Ludlow communities. *Dalmanites myops*, whose cranidia reach 4 cm in size, comprises 90% of this trilobite fauna. It is the most ubiquitous species of the association, and has been recorded in every sample from the mudstone facies. *Dalmanites* generally has a relative abundance of less than 5% of the total fauna, but becomes a dominant member of the association in the laminated shale facies. High densities of *Dalmanites* within the laminated shale facies correspond to discrete bioturbated intervals (Fig. 23), and this trilobite probably had a deposit-feeding mode of life. Other characteristic trilobites of the association include *Leonaspis coronata* and *Raphiophorus parvulus*, whose cranidia are less than 1 cm in size.

Minor groups

Hyolithes forbesi, a conical shell reaching 15 mm in length, is a minor but characteristic species of the *G. obovata* Association (Figs 21 and 22). Runnegar *et al.* (1975) demonstrated that hyolithids possessed a highly-folded gut, and suggested a deposit-feeding mode of life for the group. This is compatible with the consistent occurrence of *H. forbesi* in bioturbed mudstone.

Ostracods occur sporadically in samples of the association. In the mudstone facies, measured densities range from 0 to 24 valves per 0·1 m^2. Stratigraphic patterns of density in the laminated shale facies are shown in Fig. 23.

Crinoid ossicles are also sporadically present through the *G. obovata* Association, rarely occurring as articulated stem segments up to 2 cm in length. Observed columnals are 2 mm or less in diameter, and indicate very small individuals. Measured densities in the mudstone facies range from 7 to 20 columnals per 0·1 m^2, which is below the normal density for brachiopod valves. Crinoid individuals would thus have comprised far less than 1% of the fauna at any sampling station. In the laminated shale facies, ossicles of both calyx and stem occur on rare, small, circumscribed bedding surfaces, suggesting *in situ* decay of single individuals.

Bryozoa, solitary corals and tentaculitids occur very rarely in the *G. obovata* Association. The species of these groups are more abundant in other communities, and probably existed in the mudstone facies and laminated shale facies below the optimum of their environmental range. Extremely rare fossils known from the Elton Beds are large ceratiocarid crustaceans (Jones & Woodward 1888–89) and the echinoid *Myriastiches gigas* Sollas (Lister & Downie 1967).

Substrate and feeding relations in the association

Hancock *et al.* (1974) and Calef & Hancock (1974) considered great water depth and very low food supply as the most important environmental factors relating to the fauna of the Elton Beds and similar communities of the British Wenlock. The small size of brachiopod individuals in such communities was their chief evidence of low food supply. However, Lister (1970) recorded high densities of arcritarchs from the Elton Beds, indicating that the phytoplankton-derived food supply of the *G. obovata* Association may not have been extremely low.

The mudstone facies of the Elton Beds includes no sand and over 50% of clay, and is the most thoroughly bioturbated of Ludlow shelf sediments (Pl. 1, fig. 5). These relations indicate a soft, continuously reworked substrate, and suggest an alternative explanation for the small size of brachiopods in the *G. obovata* Association. Bokuniewicz *et al.* (1975 : 277) gave a formula for the depth to which an epifaunal animal would sink into soft sediment. A brachiopod maintaining a constant shape factor must decrease its radius and wet weight (that is, its overall size) to prevent increased sinking as it occupies bottoms of progressively lower hardness. Most brachiopods in the *G. obovata* Association could have elevated the commissure only a few mm above the bottom, and even a small amount of sinking into the substrate would have been critical. Thus small size would have been an important adaptation to a soft mud bottom.

Fürsich & Hurst (1974) stated that Spiriferida and Pentamerida maintained larger individuals relative to other brachiopods in 'deep water' environments of low food supply because they had more efficient lophophores. However, this feeding-related size factor also appears to be modified by substrate conditions. In the Elton Beds, which Fürsich & Hurst (1974) consider to represent a 'deep-water', nutrient-poor environment (the Ludlow *Dicoelosia* Community of their report), the dominant Spiriferida and Pentamerida are *Glassia obovata*, ? *Protozeuga* sp. and *Parastrophinella* sp. These species are less than 1 cm in mean size, and no larger than species of other brachiopod orders in the association.

The stratigraphic interval in section 5I where brachiopods decline in density and relative abundance and nuculoids become the community dominants may also be related to substrate conditions. This interval (Fig. 21) may represent conditions of extremely liquified sediment, suitable for nuculoids, but too soft to support brachiopods at the sediment surface. Rhoads & Young (1970) showed that modern nuculoid bivalves contribute to liquefaction of muddy substrates by their burrowing and feeding activities, and directly inhibit colonization by epifaunal suspension-feeders. Similar competitive exclusion and substrate conditioning may have occurred at the peak of nuculoid abundance in the *G. obovata* Association.

Occurrence of the association in the laminated shale facies

Stratigraphic profiles of the *G. obovata* Association in the laminated shale facies are shown in Fig. 23. Rare, isolated specimens of *Dalmanites*, *Nuculites*, *Praenucula*, *Cymbularia*, *Sphenosphaera* and *Parastrophinella* occur sporadically throughout most parts of the shale. Density of these forms is so low that they were probably not reproducing populations, but pelagically-recruited, non-reproducing individuals at their extreme limits of environmental tolerance. Indeterminate bivalves less than 1 mm in size are locally abundant in the shale (Fig. 23), and may represent early-shelled larvae of nuculoids or other benthic bivalves which died *en masse* shortly after settling on the laminated mud bottom. As discussed above, p. 193, low oxygen concentrations were probably the restrictive factor for bottom life in this environment.

The densest occurrences of *Dalmanites* and other members of the *G. obovata* Association in two intervals of bioturbated mudstone within the laminated shale facies (Fig. 23) probably indicate times of temporarily well-oxygenated conditions. Calef & Hancock (1974) made one collection from this type of fauna in the Middle Elton Beds near Ludlow. This sample was assigned to their '*Visbyella* Community', based on the supposed endemic occurrence of '*Visbyella trewerna*' and '*Clorinda dormitzeri*'. These taxa are synonomous with the *Resserella sabrinae nunfieldensis* and *Parastrophinella* sp. of this report. Both species occur throughout the Elton Beds of all shelf areas studied here, and they cannot be used to define a separate community in the shelf edge area around Ludlow. There is no evidence for a '*Visbyella* Community' in Ludlow sediments of the Welsh Borderland.

The statement by Calef & Hancock (1974) that their '*Visbyella* Community' represents 'the deepest limits of Silurian benthonic life' is also inapplicable to Ludlow faunas. The laminated shale facies of the Ludlow area is intercalated within a succession of shelf sediments (Fig. 3, p. 182), and cannot represent abyssal or very great depths. Sparse Silurian benthic faunas in laminated shales have also been related to extremely deep water by Boucot (1975) as 'benthic assemblage 6'. This interpretation ignores the importance of low oxygen levels in producing laminated shales with impoverished faunas, and is part of the undue emphasis which Silurian palaeoecologists have placed on water depth. Oxygen minima may operate over a wide depth range, as discussed by Shäfer (1972).

Transition from the *Glassia obovata* Association to the *Mesopholidostrophia laevigata* Association

Where the mudstone facies grades into the overlying bioturbated siltstone facies or calcisiltite facies, an extensive stratigraphic transition in fauna occurs between the *Glassia obovata* Association of the Elton Beds and the *Mesopholidostrophia laevigata* Association of the Lower Bringewood Beds. Discontinuous sections of this transition have been measured near Ledbury and Perton. The strata involved are assigned to the Upper Elton Beds on the basis of abundant *Pristiograptus tumescens* (Wood) in the Perton sections.

This ecological gradation is characterized by the disappearance of several characteristic fossils of the *G. obovata* Association. *Parastrophinella* sp. disappears relatively early, followed in order by *Glassia obovata*, *Leonaspis coronata*, ? *Protozeuga* sp., *Hyolithes forbesi* and *Praenucula* sp. Other forms, such as *Isorthis* and *Skenidioides*, decline in relative abundance. Bryozoa, stropheodontid brachiopods, *Sphaerirhynchia*, *Atrypa* and several other characteristic forms of the *M. laevigata* Association appear within the transitional interval in low but stratigraphically increasing abundances. Profiles of this transition are shown in Figs 19 and 21, and full faunal data are given in Table 15 of Appendix 3, pp. 263–6.

The transition between the *G. obovata* Association and *M. laevigata* Association occurs through a stratigraphic interval of about 30–50 m, and is completely gradual, reflecting a corresponding gradual change in sediment in which clay content decreases, bioturbation becomes less ubiquitous, swell lags of shells begin to appear and the amount of calcite cement increases. A change to a cleaner, less liquefied substrate under more agitated waters is indicated. The delimitation of a 'transition fauna' between the two associations in Figs 19 and 21 is a matter of convenience, and its boundaries are arbitrarily located at gaps in the stratigraphic exposure.

Mesopholidostrophia laevigata Association

The *M. laevigata* Association occurs in the calcisiltite facies and bioturbated siltstone facies of the Lower and Upper Bringewood Beds. It is the most diverse Ludlow shelf community, and is dominated by brachiopods and bryozoa. Swell lag assemblages of the *M. laevigata* Association are illustrated in Plate 4. Figs 16, 17, 19 and 20 show faunal profiles of the association, and complete faunal data are given in Appendix 3, Tables 15 and 18, pp. 270–1.

Brachiopods

Strophomenida are the most conspicuous brachiopods of the association, reaching sizes of 4 cm and comprising about one third of the total fauna. The 11 species present show a variety of adaptations for reclining upon soft sediment. These include stabilization by spines (*Protochonetes*), weighting of the posterior part of the ventral valve (*Mesopholidostrophia*), dorsal elevation of

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Plate 4

Mesopholidostrophia laevigata Association

Fig. 1. Sample 3A102, showing: a. *Mesopholidostrophia laevigata* (J. de C. Sowerby); b. *Leptostrophia filosa* (J. de C. Sowerby); c. encrusting bryozoan; d. *Sphaerirhynchia wilsoni* (J. Sowerby); e. *Atrypa reticularis* (Linnaeus); f. *Amphistrophia funiculata* (M'Coy). BB 73378. × 1·5.

Fig. 2. Sample 3A67, showing: c. encrusting bryozoan; g. *Dalejina hybrida* (J. de C. Sowerby). BB 73379. × 2.

Fig. 3. Sample 3A102, showing: b. *L. filosa*; c. encrusting bryozoan; e. *A. reticularis*; f. *A. funiculata*; h. '*Schuchertella*' sp.; i. *Isorthis clivosa* Walmsley. BB 73380. × 1·5.

Fig. 4. Sample 3A102, showing: a. *M. laevigata*; b. *L. filosa*; c. encrusting bryozoan; e. *A. reticularis*; i. *I. clivosa*; k. *Cypricardinia subplanulata* Reed; m. *Strophonella euglypha* (Hisinger); n. *Euomphalus* sp. BB 73380. × 1·5.

Fig. 5. Sample 3A67, showing: c. encrusting bryozoan; e. *A. reticularis*; g. *D. hybrida*; h. '*Schuchertella*' sp.; j. *Dalmanites myops* (König); l. *Howellella elegans* (Muir-Wood); o. unidentified conical shell; p. *Mytilarca siluriana* Reed. BB 73381. × 2.

All figures are of latex casts of 'swell lag' surfaces, coated with ammonium chloride, from the Lower Bringewood Beds at Woodbury Quarry. BB numbers refer to the brachiopod collections of the Department of Palaeontology, British Museum (Natural History).

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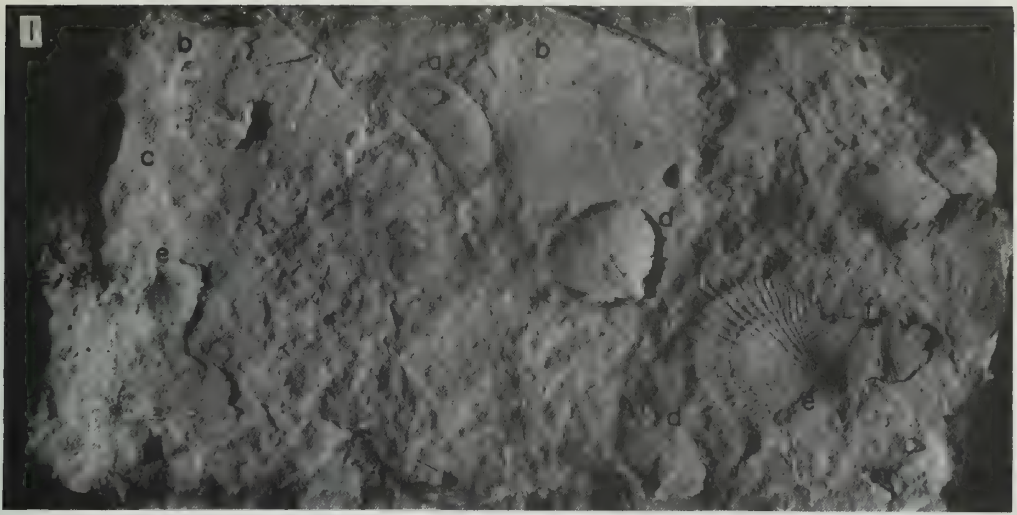

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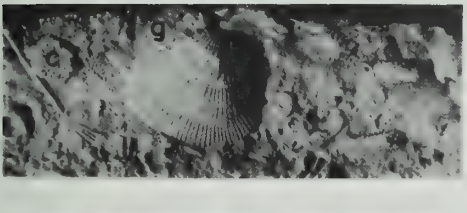

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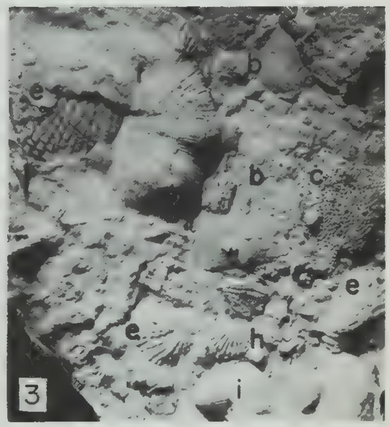

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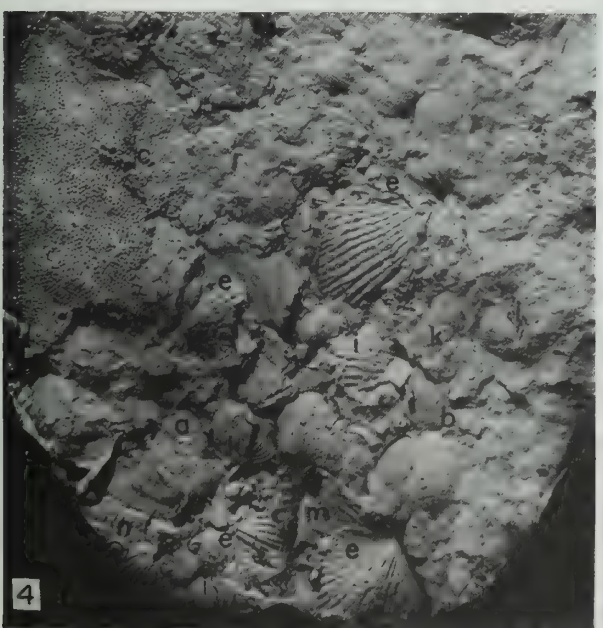
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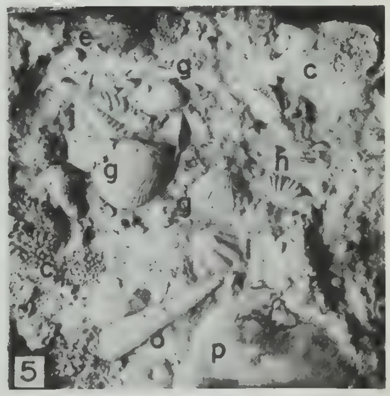


the commissure (*Strophonella*, *Amphistrophia*, *Leptaena*) and stabilization by a pedicle ('*Schuchertella*', *Lepidoleptaena*). Shell occurrence indicates that the freely reclining strophomenides must have been periodically disturbed by minor water agitation. Of 52 whole and disarticulated strophomenides in Woodbury Quarry, 63% were observed with convex sides upwards, 29% had convex sides downwards and 8% were orientated obliquely to bedding. In life orientation, individuals would have rested with the convex valve downwards and the commissure directed away from the substrate. The orientation data suggest that they were susceptible to frequent overturning to a hydrodynamically stable position. Abundance of strophomenides in the association indicates that this could not have had an adverse effect on their survival, and overturned individuals may have been able to right themselves by rapid snapping of the valves.

Shagamella ludloviensis is a strophomenide less than 5 mm in size which occurs throughout sections bearing the *M. laevigata* Association. It is usually present in low abundance, but shows very high densities locally. It also occurs abundantly in the laminated shale facies of the Upper Elton Beds near Ludlow, where it is associated with graptolites in the absence of a well-developed benthic fauna. *Shagamella ludloviensis* is considered, like *Aegiria*, to have had an epiplanktic mode of life. Its occurrences are given in Appendix 3, but it is not included in calculations or faunal profiles for the *M. laevigata* Association.

Twenty-one other brachiopod species in the association show adaptations for pedunculate or reclining modes of life. *Isorthis* and *Howellella* are the most common pedunculate forms, and *Gypidula*, *Sphaerirhynchia* and *Atrypa* are the most important of reclining brachiopods. Although no single brachiopod species dominates extensive stratigraphic intervals of the *M. laevigata* Association, any one of several species may predominate in single samples. These patterns of dominance show continuous fluctuations in stratigraphic sections (Fig. 17). In most species, temporary peaks of abundance are attained through gradual stratigraphic increases, followed by a decline and a stratigraphic interval of low abundance or absence. Complete cycles for a species occur over 5–10 m vertical intervals. These patterns of changing abundance are tested against a model of ecological succession in a following section.

Bryozoa

Bryozoa comprise 7% of the association, according to the method of counting, and occur with brachiopods on nearly every surface of rock (Plate 4). Owen (in Holland *et al.* 1963) listed 21 bryozoan species from the Lower Bringewood Beds of the Ludlow area, which indicates their high diversity in this community. Lamellose colonies encrust a high proportion of shell fragments, especially those of larger brachiopods. Colonies are less than 2 mm in height and in some cases extend around both surfaces of the shell fragment, indicating successful survival when the fragment was overturned. These forms are also present on the exteriors of whole brachiopods, and must have grown in part during the life of the host.

Other lamellose colonies grew partially or wholly on the sediment bottom. These forms have irregular bases corresponding to bottom configuration, and probably played a minor role in binding the sediment surface. They reach breadths of 3 cm, and vary from sheet-like to hemispherical in form. Globular colonies reaching 15 mm in diameter show growth on all surfaces, and could have survived if shifted in any orientation. Ramose branches extended from all colony forms, as indicated by broken basal attachments. Ramose colonies, reaching at least 4 cm in height, also grew directly upward from anchorages to shell fragments. Rare fragments of fenestrate bryozoa have also been found, but their relation to the substrate is unknown.

Molluscs

Bivalves comprise only 2% of individuals in the association, but are represented by at least 22 species. Patterns of occurrence can be obtained from Table 18. Most species occur in small numbers at widely separated stratigraphic intervals, and must have had very small, geographically restricted populations. Only *Cypricardinia subplanulata* and *Actinopteria sowerbyi* show a fairly consistent pattern of occurrence.

Nine species of gastropods also comprise about 2% of the association. *Bembexia lloydii*, *Leptozone striatissima* and *Oriostoma* sp. are characteristic forms, and reach maximum diameters of 2–3 cm. Rare cephalopods in the association are mostly ornamented forms like those interpreted as nektobenthic predators in the *G. obovata* Association.

Trilobites

Trilobites are very minor members of the *M. laevigata* Association, but occur continuously throughout stratigraphic profiles (Fig. 17). *Dalmanites myops* comprises about 40% of the trilobite fauna, and other species include encrinurids, calymenids and proetids. Five trilobite species have been found in this community during the present study, but additional forms in the Bringewood Beds have been listed by Holland *et al.* (1963) and Shergold & Shirley (1968).

Minor groups

Tentaculites, cornulites and conularids are represented by single species in the *M. laevigata* Association, and occur sporadically in samples in abundances of less than 1%. Many of the rare ceratiocarid crustaceans described by Jones & Woodward (1888–89) were probably also members of this community.

Solitary trochoid corals form 1·7% of individuals collected from the association. They show a fairly consistent stratigraphic occurrence, and reach diameters of 15 mm. These corals have been treated as a single taxon in diversity calculations, but have not been studied in section, and may represent more than one species. *Rhabdocyclus porpitoides* is a less common solitary coral. Syringoporid colonies are present on brachiopod shells and fragments, and colonies reaching 3 cm across also occur freely within the sediment.

Ostracods are locally common in the *M. laevigata* Association, and can be seen on all bedding surfaces illustrated in Plate 4. Shergold & Shirley (1968) listed several species occurring in the Lower Bringewood Beds of the Wenlock Edge area.

Crinoid columnals have an average density in bioturbated siltstone of about 4 per 0·1 m^2. Living individuals may have been more abundant than suggested by this figure, however, as crinoid columnals are abundant in shell beds of the bioturbated siltstone facies (Pl. 1, fig. 1), and have been preferentially sorted and concentrated. Columnals reach 9 mm in diameter, indicating the largest crinoid individuals in any of the Ludlow shelf communities. Columnals of this size are present in whole camerate individuals from the Wenlock Limestone of Dudley which reach heights of at least 20 cm.

Lawson (1973*a*) recorded the echinoid *Echinocystites pomum* Thomson and the ophiuroid ? *Urosoma hirudo* (Forbes) from the Lower Bringewood Beds of the Aymestrey area, which contain the *M. laevigata* Association.

Trophic structure of the *M. laevigata* Association

The *M. laevigata* Association contains the greatest trophic differentiation of the communities studied here, and emphasizes several problems pertinent to trophic analysis of Ludlow faunas. Suspension-feeding brachiopods are predominant, followed in abundance by suspension-feeding bryozoa and a number of other suspension-feeding groups, including bivalves, corals, crinoids, and possibly tentaculites and cornulites. Life habits and sizes of individuals in these groups indicate stratified levels of feeding above the sediment surface. Crinoids, possibly extending to 20 cm in height, were the highest feeders, followed by the tallest of ramose bryozoan colonies. These feeding levels were probably rather sparsely populated. Trochoid corals, various bryozoa and large brachiopods occupied a feeding level 1–2 cm above the bottom, and sheet-like bryozoa, small brachiopods and shallowly-buried bivalves fed very near the sediment surfaces. These were the most heavily utilized feeding levels in the community. Gastropods may have exploited a variety of feeding strategies, and cephalopods, present in very low abundance, have an acceptable occurrence pattern as predators.

On the basis of body fauna, deposit-feeding would appear to be limited to only a few per cent of community members, including nuculoid bivalves, possibly ostracods, and possibly many of the trilobites. However, the presence of *Chondrites* and extensive deformative bioturbation indicates a very active soft-bodied burrowing fauna. The majority of these burrowers were probably deposit feeders, and the *M. laevigata* Association can thus be considered as having had a mixed trophic structure with both epifauna and infauna abundant. Other Ludlow shelf communities show this same situation, although they probably had much less stratification of suspension feeding. *Chondrites* and deformative bioturbation indicate abundant deposit feeding in all sedimentary facies. The number of soft-bodied organisms or amount of deposit feeding relative to body fossils cannot be measured, however, and to this extent the trophic structure in Ludlow communities cannot be treated in a precise or quantitative manner.

Upper boundary of the *M. laevigata* Association

As indicated in Fig. 12, the *M. laevigata* Association is overlain by the *Sphaerirhynchia wilsoni* Association. In sections 3A and 4B, the stratigraphic boundary of these associations is marked by the disappearance or sharp drop in abundance and frequency of occurrence of species of '*Schuchertella*', *Strophonella*, *Amphistrophia*, *Mesopholidostrophia*, *Leptostrophia*, *Gypidula* and *Eospirifer* (Figs 17 and 19). At or slightly above the level of these disappearances and reductions, *Sphaerirhynchia wilsoni*, '*Camarotoechia*' *nucula* and *Howellella elegans* increase in abundance and become the dominant species of the *S. wilsoni* Association. These changes occupy a stratigraphic interval of about 5 m, and represent a permanent alteration in fauna. They occur within either the bioturbated siltstone facies or calcisiltite facies, and are not accompanied by any apparent changes in grain size, sediment composition, or sedimentary structures. The environmental cause of this transition is not clear, and it does not affect bryozoa, bivalves, gastropods, trilobites and minor phyla.

A clearly recognizable boundary between the *M. laevigata* Association and *S. wilsoni* Association is also seen in section 2D near Ludlow (Fig. 16). The same disappearances of brachiopod species noted above occur, and *Dayia navicula*, *Hyattidina canalis*, *Isorthis orbicularis* and '*Camarotoechia*' *nucula* either appear or sharply increase in abundance, to define the base of the *S. wilsoni* Association. Unlike the previous examples, changes in the non-brachiopod fauna also occur at this level, most notably a disappearance of corals and a marked reduction in abundance and diversity of bryozoa (Fig. 16). These changes occur through a stratigraphic interval of about 2 m within a minor development of the 'Aymestry Limestone' facies. Although they occur within a single rock type, they relate broadly to a sedimentary change, as most of the *M. laevigata* Association in this section, below the limestone, is contained within the bioturbated siltstone facies, while most of the *S. wilsoni* Association, above the limestone, occurs within the coquinoid siltstone facies. Change in substrate and increased sedimentation rates were probably responsible for the disappearance of corals, reductions in bryozoa, and alteration in the brachiopods.

Sphaerirhynchia wilsoni Association

The *S. wilsoni* Association is present in the bioturbated siltstone facies, calcisiltite facies, 'Aymestry Limestone' facies and coquinoid siltstone faces, which is the widest environmental range of any Ludlow shelf community in the study area. It has two separate stratigraphic occurrences, a lower phase in the Lower Bringewood Beds of the Perton, Ledbury, and Woodbury Quarry sections, and an upper phase in the Lower Leintwardine Beds of all areas studied (Fig. 12). Ecological distinctions between the two phases are discussed below, p. 230. Faunal profiles of the *S. wilsoni* Association are shown in Figs 10 and 16–20, and checklists of species are given in Appendix 3, Tables 15, 16 and 19.

Brachiopods

In the lower phase of the *S. wilsoni* Association, 27 species of brachiopods comprise 81% of the total fauna. The dominant forms are *Sphaerirhynchia*, *Atrypa*, *Howellella*, '*Camarotoechia*', *Dalejina* and *Isorthis*. The separation of *Isorthis orbicularis* in the *S. wilsoni* Association from *Isorthis clivosa* in the *M. laevigata* Association is a matter of nomenclatural convenience. Although morphologically distinct at the extremes of their stratigraphic ranges, populations of these species grade continuously into one another through the Bringewood Beds. Stratigraphic patterns of abundance of most brachiopod species in the lower phase of the *S. wilsoni* Association are similar to those of brachiopods in the *M. laevigata* Association, and consist of gradual, stratigraphically peaking cycles of abundance. The lower phase is also characterized by the occurrence in low abundance of some of the previously dominant brachiopods of the *M. laevigata* Association.

In the upper phase of the association, within the Lower Leintwardine Beds, brachiopod diversity decreases to 19 total species. Abundance patterns of brachiopods become more unpredictable and reach greater extremes, and large fluctuations in composition of fauna occur over very short stratigraphic intervals, as shown in Figs 16, 17, 18 and 20. Any one of eight brachiopod species, including representatives of *Salopina*, *Isorthis*, *Protochonetes*, *Shaleria*, *Sphaerirhynchia*, '*Camarotoechia*', *Hyattidina* and *Howellella*, may comprise over 70% of the fauna in single samples. This pattern was investigated in small-scale detail in section 4A, as shown in Fig. 10. The results show that the extreme fluctuations in relative abundances occur over stratigraphic distances of only centimetres. Lateral sampling of bedding surfaces (Figs 7 and 9) shows that major changes in brachiopod fauna can occur over only a metre at the same stratigraphic horizon.

Profiles of brachiopod abundances in the upper phase, as constructed from samples at 1-m intervals, present only the general pattern of faunal variation in the Lower Leintwardine Beds. They suggest, but do not show in its entirety, the complexity of this variation, and sampling of the same section at different points would produce a quantitatively different pattern. Even a cm by cm sampling of the upper phase would be valid only for the particular stratigraphic line of transect, and would differ from a profile constructed a few metres laterally. Although part of these widely-fluctuating abundances of brachiopod species in the upper phase are taphonomic results of the occurrence of storm shell beds, the same extreme unpredictable changes in abundances are seen within disturbed neighbourhood assemblages.

Lawson (1975) also noted this extreme fluctuation of brachiopod species in the Lower Leintwardine Beds, and suggested that each band of shells dominated by a different single brachiopod species might be considered a separate community. This suggestion is to equate a community with a single-species population, and carried to its extreme, might recognize 8 or even 8! communities within the Lower Leintwardine Beds. The view taken here is that the upper phase of the *S. wilsoni* Association represents a single community dominated by several 'opportunistic' brachiopod species, each adapted to a strategy of temporary, intensive reproduction. This view follows the transect definition of a community, and not the definition of a community by some specified proportion of species. The basic ecologic unity of the upper phase of the *S. wilsoni* Association, according to the transect approach, can be easily seen in Figs 17 and 18.

Shagamella ludloviensis, which earlier was interpreted as an epiplanktic species, occurs throughout both phases of the *S. wilsoni* Association. In the upper phase, individuals reach 1 cm in size and show a convergence in shell form with *Protochonetes ludloviensis*, a definitely benthic form. These populations of large *Shagamella* in the Lower Leintwardine Beds show the same pattern of extreme fluctuations in abundance as those discussed above, and probably should be treated as benthic in mode of life. *Shagamella* is shown in faunal profiles for the *S. wilsoni* Association in Figs 18 and 20, but omitted from other diagrams. A complete record of its occurrence is given in Appendix 3.

Bryozoa

In the lower phase, bryozoa comprise 9% of the total fauna, and show the same diversity and morphological forms as those in the *M. laevigata* Association. Bryozoa decline to an average abundance of 3% of the fauna in the upper phase, and are represented mainly by ramose growth forms, with very few of the varied colonies described earlier. Owen (in Holland *et al.* 1963) listed seven bryozoan species from the Lower Leintwardine Beds of the Ludlow area, which indicates the lowered diversity of the group in the upper phase of the *S. wilsoni* Association.

Molluscs

Bivalves comprise 2% of the fauna in the lower phase, and the 17 species recorded are forms from the *M. laevigata* Association, with the same sporadic pattern of occurrence. Bivalves increase in abundance to 5% of the fauna in the upper phase, and 15 species have been recorded, a few different from those in the lower phase bivalve fauna. Bivalves reach local abundances of 20% of the fauna in the upper phase, and are dominated by '*Paracyclas*' *insueta*, *Nuculites antiqua*, *Pteronitella retroflexa* and *Sedgwickia amygdalina*. Individuals of these species reach larger sizes than most bivalves in preceding communities, and the latter two commonly attain lengths of 2–3 cm.

The gastropod fauna of the lower phase is also a continuation of that of the *M. laevigata* Association, and occurs continuously throughout the stratigraphic sections in low abundance (Figs 17 and 19). Six species of gastropods in the upper phase of the association have been recorded in a much more sporadic stratigraphic pattern of occurrence. Cephalopods comprise less than 1% of both lower and upper phases of the *S. wilsoni* Association.

Trilobites

Trilobites comprise 1·4% of individuals collected from the lower phase, and occur fairly continuously in stratigraphic sections. They comprise the same species as in the *M. laevigata* Association, and are dominated by *Dalmanites myops*. This fauna essentially disappears within the upper phase of the association, which contains only rare proetids and *Acastella spinosa*.

Minor groups

The same two species of tentaculite and cornulite occur sporadically throughout both lower and upper phases, comprising less than 1% of the total fauna. They are joined in the upper phase of the association by the tubiculous annelid *Serpulites longissimus*, which is also rare. The coral fauna of the *M. laevigata* Association is present in small numbers in the lower phase of the *S. wilsoni* Association, and disappears in the upper phase. Ostracods occur sporadically throughout both phases, but are not consistently present. They become extremely abundant at stratigraphically isolated intervals in the upper phase, numbering several hundred valves per 0·1 m^2. Kjellesvig-Waering (1961) reported rare eurypterids from stratigraphic horizons which bear the upper phase of the *S. wilsoni* Association. Crinoid columnals are locally abundant in transported shell beds of both phases, but number less than 10 per 0·1 m^2 in bioturbated sediment.

A rich fauna of complete crinoids, echinoids and asteroids is known from the Lower Leintwardine Beds of the Leintwardine area (Ramsbottom 1958, Hawkins & Hampton 1927, Spencer 1914–40). This fauna lived at the sites of channel bottoms (Whitaker 1962), and must have been preserved by very rapid sedimentation. Stratigraphically associated brachiopod faunas represent the upper phase of the *S. wilsoni* Association. Species of the Leintwardine echinoderm fauna may have been more widely distributed over shelf areas of the coquinoid siltstone facies, but if so have not been recognized because of complete disarticulation of their skeletal elements.

Ecological distinction of lower and upper phases

The coquinoid siltstone facies, containing the upper phase of the *S. wilsoni* Association, represents a higher energy environment with more rapid sedimentation than the bioturbated siltstone facies and calcisiltite facies, which contain the lower phase of the association. Most forms which decrease in abundance or disappear in the upper phase were probably adversely affected by increases in sedimentation rate. The disappearance of corals can be best explained in this manner, as well as the decline in diversity and abundance of bryozoa. The predominant ramose forms of bryozoa in the upper phase could have coped with sedimentation by upward growth, which would not have been possible for the sheet-like and globular colonies prevalent in the lower phase.

Upper phase brachiopods also show proportional shifts in life-habit groups with the incoming of the coquinoid siltstone facies. Many strophomenides and reclining brachiopods disappear, and rhynchonellides, with commissural deflections to minimize sediment intake, become the most consistently abundant forms in the upper phase. No brachiopod, however, could have withstood the periodic storm deposition of laminated silt. The 'opportunistic' population strategies of upper phase brachiopods, which involved high reproductive potentials and limited time spans at single sites, were probably as important an adaptation as shell form in the environment of the coquinoid siltstone facies. This is emphasized by local abundance in the coquinoid siltstone facies of *Hyattidina canalis*. This brachiopod possesses no ribbing or commissural deflections, and has an incurved beak which would have precluded or restricted the amount of pedicle attachment. According to shell form alone, it would seem best adapted to a quiet environment of low sedimentation rate (Fürsich & Hurst 1974). It is almost exclusively restricted to the coquinoid siltstone facies of the Leintwardine Beds, however, and was probably able to survive by an ability to maintain transient but dense populations.

Atrypa reticularis – coral Association

The lower and upper phases of the *S. wilsoni* Association are separated stratigraphically by the development of the *Atrypa reticularis* – coral Association, as shown in Fig. 12. The *A. reticularis* – coral Association occurs in the 'Aymestry Limestone' facies of the Upper Bringewood Beds near Perton, at Ledbury and at Woodbury Quarry, and is a low-diversity community dominated by its eponyms. It represents a distinct stratigraphic anomaly in the ecological development of the inner shelf faunas. Faunal profiles and checklists for the *A. reticularis* – coral Association are given in Figs 17, 18 and 20 and Table 15 of Appendix 3.

Brachiopods

Atrypa reticularis is the only common brachiopod of the association, and comprises 45% of the sampled fauna. Its size range, generally from 15 to 30 mm, is the same as that in other communities. *Atrypa* fluctuates in abundance within the association, ranging from less than 5% to over 70% of individuals in single samples. Other brachiopods in the association are species which are more common in the lower and upper phases of the *S. wilsoni* Association. Although many brachiopod species of the *S. wilsoni* Association range through the *A. reticularis* – coral Association, their frequency of occurrence and abundance become very restricted in this interval, as can be seen in Fig. 17.

Corals

The coral fauna of the association consists almost wholly of the solitary trochoid forms, found also in the Lower Bringewood Beds, ranging from 15 to 20 mm in diameter. They comprise 16% of individuals sampled, but fluctuate widely in abundance through sections, reaching 70% of the fauna in local, disturbed neighbourhood assemblages. Trochoid corals were entered as a single 'species' in the diversity calculations, sections for taxonomic study not having been prepared. Although they would appear to be rare in the Woodbury Quarry profile of the association (Fig. 17), an abundant occurrence was observed outside the sampling intervals.

A single *in situ* favositid colony, 30 cm in breadth, was observed within the 'Aymestry Limestone' facies of the Upper Bringewood Beds on a face of Perton Quarry.

Minor groups

Bryozoa comprise 15% of the association, and consist of the same colony forms as described for the *M. laevigata* Association. Hemispherical colonies of *Monotrypa*, reaching 3 cm in diameter, are one of the most common bryozoans. Crinoid ossicles are locally common, and portions of stems reaching 5 cm in length occur. The gastropod *Oriostoma*, comprising about 4% of individuals, is another common member of the association. Small calcareous algae are present in thin sections of samples.

Other groups in the association comprise well below 1% of the fauna, and consist of species more commonly found in the *S. wilsoni* Association. These groups include bivalves, cephalopods, tentaculites and trilobites, and are listed in Appendix 3.

Anomalous nature of the association

The appearance of the *A. reticularis* – coral Association in shelf sections correlates with the development of the low-energy 'Aymestry Limestone' facies, and is marked by a great decline in density of fossils. In the Upper Bringewood Beds at Perton Quarry, the *A. reticularis* – coral Association occurs with an average density of about 20 shells per m^2. This is far below average densities for disturbed neighbourhood assemblages of the underlying lower phase of the *S. wilsoni* Association (380 shells/m^2) and overlying upper phase of the *S. wilsoni* Association (660 shells/m^2). The drop in shell density cannot be explained by increase in sedimentation rate, as it occurs within a fine-grained limestone showing no evidence of current deposition. Diagenetic factors can also be excluded because of good preservation of fossils and representation of many phyla. The low shell density in the *A. reticularis* – coral Association indicates a substantial drop in biotic productivity relative to stratigraphically adjacent phases of the *S. wilsoni* Association.

This drop in productivity is not accompanied by the appearance of any species new to the depositional area. Most forms from the preceding community disappear or become reduced in numbers, and a few increase in relative abundance, but not in overall density, to become the dominants of the *A. reticularis* – coral Association. The density and species changes, which mark the upper and lower boundaries of the association, are gradual and occupy stratigraphic intervals of 2–5 cm. These relations can be seen in Fig. 17.

The *A. reticularis* – coral Association does not represent a 'new 'community, but rather a restricted assemblage of forms from the lower phase of the *S. wilsoni* Association. It is a stratigraphic interruption in what would otherwise be a continuous ecological transition between the lower and upper phases of the *S. wilsoni* Association. This reflects the sedimentary interruption of the succession of terrigenous facies by the Upper Bringewood carbonates, which was discussed in the sedimentology section. The *A. reticularis* – coral Association is related in part to this change from a silty to a lime mud substrate.

The appearance and taxonomic restriction of the association is also related to the formation of a barrier system at the shelf edge, as detailed earlier. Shelf-edge barriers offer an explanation for the quiet-water features of the inner shelf 'Aymestry Limestone' facies, and probably produced very restricted water circulation, with lessened influences of basin and oceanic waters. This would not have affected salinity, as indicated by the phyla present in the inner shelf area, but could have altered conditions of phytoplankton abundance and nutrients available to benthic organisms.

Plate 5

Sphaerirhynchia wilsoni Association

Fig. 1. Sample RW4 (section 1C), showing: b. *Isorthis orbicularis* (J. de C. Sowerby); c. *Protochonetes ludloviensis* Muir-Wood; d. '*Camarotoechia*' *nucula* (J. de C. Sowerby); e. *Salopina lunata* (J. de C. Sowerby); g. *Sphaerirhynchia wilsoni* (J. Sowerby). BB 73382. × 1·5. Lower Leintwardine Beds near Millichope Park.

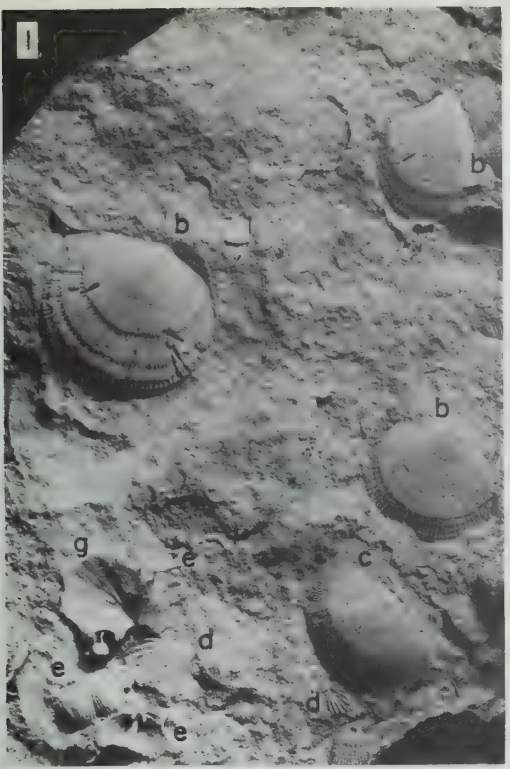
Protochonetes ludloviensis Association

Fig. 2. Sample 2B2, showing: a. *Nuculites antiqua* (J. de C. Sowerby); c. *P. ludloviensis*; d. '*C.*' *nucula*; e. *S. lunata*. BB 73383. × 1·5. Upper Whitcliffe Beds, Ludlow.

Fig. 3. Sample 4A3, showing: c. *P. ludloviensis*; d. '*C. nucula*; f. ramose bryozoan fragment. BB 73384. × 1·5. Whitcliffe Beds, Frith Wood, near Ledbury.

Fig. 4. Sample 2B2, showing: c. *P. ludloviensis*; e. *S. lunata*. BB 73385. × 1·5. Upper Whitcliffe Beds, Ludlow.

All figures are of latex casts coated with ammonium chloride. BB numbers refer to the brachiopod collections of the Department of Palaeontology, British Museum (Natural History).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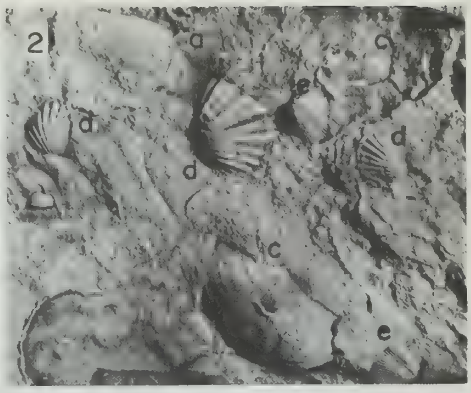
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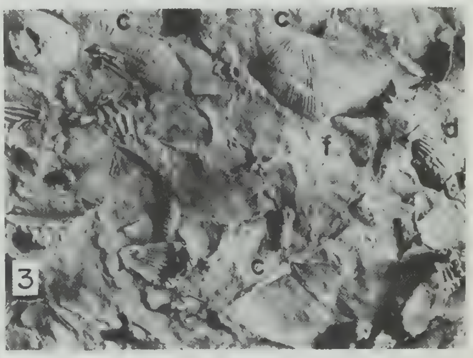
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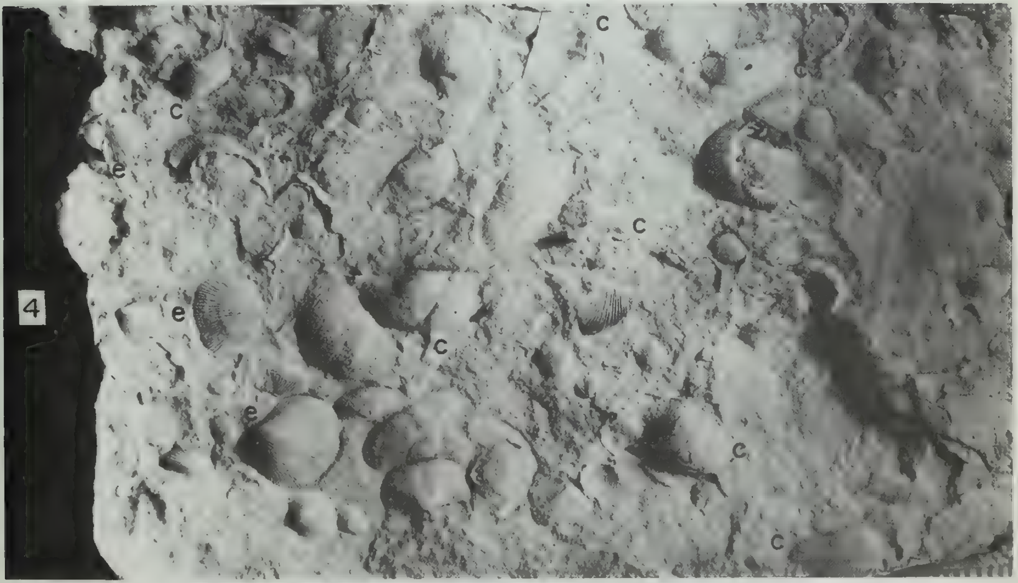
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Shaleria ornatella Association

The *S. ornatella* Association is the fauna which defines the Upper Leintwardine Beds in shelf areas, and it is confined to a restricted vertical interval of the coquinoid siltstone facies. This community occupies a consistent stratigraphic position between the upper phase of the *Sphaerirhynchia wilsoni* Association and the *Protochonetes ludloviensis* Association as shown in Fig. 12. It interrrupts what would otherwise be a continuous gradation between these two communities, and is another ecological anomaly in shelf sections. Faunal profiles of the *S. ornatella* Association are shown in Figs 16–18 and 20, and counts for each species are given in Appendix 3, Tables 16 and 19.

Brachiopods

Shaleria ornatella is a free-lying strophomenide which occurs in low abundance throughout the *M. laevigata* Association, is rare in most parts of the *S. wilsoni* Association and returns in great abundance across the Welsh Borderland in the Upper Leintwardine Beds. *Leptaena depressa* and *Lepidoleptaena* sp. are other common Upper Leintwardine strophomenides which are also found throughout the *M. laevigata* Association, returning to shelf sections after an interval of rarity in the Lower Leintwardine Beds. These two species are adapted to partial burial in soft sediment, with a long trail elevating the commissure above the substrate. They are externally homeomorphic, and *Lepidoleptaena* is distinguished by the presence of a small pedicle foramen.

Isorthis clivosa is another common brachiopod of the *S. ornatella* Association. Ludlow *Isorthis* in the Welsh Borderland shows a continuous, environmentally-correlated morphological change from *I. clivosa* in the Elton Beds (*G. obovata* Association) to *I. orbicularis* in the Lower Leintwardine Beds (*S. wilsoni* Association). This change is a statistical phenomenon seen in entire populations, and involves an increase in size, relative decrease in shell depth and changes in articulation structures and muscle fields. The trend is abruptly terminated with the incoming of the *S. ornatella* Association, which correlates with a disappearance of *I. orbicularis* and the reappearance of *I. clivosa*. Upper Leintwardine populations of *I. clivosa* show greatest morphological resemblance to *clivosa* populations of the Lower Bringewood Beds (*M. laevigata* Association). These statements are based on a statistical study of several hundred specimens (Hurst & Watkins 1978).

Other common brachiopods in the *S. ornatella* Association are *Salopina lunata*, *Protochonetes ludloviensis*, *Atrypa reticularis* and '*Camarotoechia*' *nucula*. All of the species mentioned show extreme small-scale stratigraphic fluctuation in relative abundances. This indicates an 'opportunistic' pattern like that discussed for brachiopods in the upper phase of the *S. wilsoni* Association. Brachiopods comprise 87% of the total fauna collected from disturbed neighbourhood assemblages of the *S. ornatella* Association.

Bivalves

Bivalves comprise 7% of the association, and are the second most abundant faunal group. Free-burrowing, epibyssate and endobyssate species are present, but the latter comprise 86% of all individuals. The bivalve fauna of the *S. ornatella* Association is a continuation of that in the upper phase of the *S. wilsoni* Association, with the same dominant species. *Cypricardinia subplanulata* and *Mytilarca siluriana*, common bivalves of the *M. laevigata* Association, appear among the bivalve fauna of the *S. ornatella* Association after an interval of absence in the Lower Leintwardine Beds.

Trilobites

Trilobites are characteristic organisms of the *S. ornatella* Association, although they comprise only 1% of collected fauna. Their continuous presence throughout sections of the Upper Leintwardine Beds contrasts with their much rarer occurrence in the upper phase of the *S. wilsoni* Association (Lower Leintwardine Beds), as shown in Figs 17 and 18. *Calymene neointermedia*, *Encrinurus stubblefieldi* and proetids are the principal forms. This trilobite fauna resembles that of the Lower Bringewood Beds in general morphologic composition. Holland *et al.* (1963) and Shergold & Shirley (1968) have discussed the stratigraphic significance of the Upper Leintwardine trilobite fauna.

Minor groups

Minor groups recorded from the *S. ornatella* Association are ramose bryozoans, gastropods, cephalopods, tentaculites, cornulites, ostracods and crinoid ossicles. Details of all but the latter two groups are given in Appendix 3.

Anomalous nature of the association

The *Shaleria ornatella* Association occupies a stratigraphic interval of about 8 m at Ludlow and 1–5 m in shelf areas to the east. This thickness of strata is much less than that occupied by other communities in the coquinoid siltstone facies, and indicates a relatively brief duration of the association. In spite of its stratigraphic restriction, the *S. ornatella* Association is present in every Upper Ludlow section in the Welsh Borderland (Holland *et al.* 1963).

As shown in Fig. 12, the *Shaleria ornatella* Association occupies a stratigraphic position between the upper phase of the *S. wilsoni* Association (Lower Leintwardine Beds) and *P. ludloviensis* Association (Whitcliffe Beds). What would otherwise be a relatively simple ecological gradation between these two communities is interrupted by the stratigraphic appearance of the *S. ornatella* Association. Both lower and upper stratigraphic boundaries of the association are distinct enough to be located within intervals of 1 m (Figs 16–18). The *S. ornatella* Association marks the brief return of several characteristic forms from the bioturbated siltstone facies lower in the succession which are absent or rare in the intervening Lower Leintwardine Beds. The total faunal aspect of the *S. ornatella* Association is unlike that of surrounding communities in the coquinoid siltstone facies, and resembles the *M. laevigata* Association in the prominence of stropheodontids, leptaenids, *Isorthis clivosa*, *Atrypa reticularis* and trilobites.

The faunal relations of the *S. wilsoni* Association and *P. ludloviensis* Association, discussed later, indicate adjacent positions along an environmental gradient. Similar environmentally-controlled, superpositional relationships of *S. wilsoni*-type communities and less diverse *P. ludloviensis*-type communities have been described from the Wenlock of the Welsh Borderland (Calef & Hancock 1974) and the Pridoli of Nova Scotia (Watkins & Boucot 1975). Counterparts of the *Shaleria ornatella* Association are not seen in these community sequences. The stratigraphic position of the *S. ornatella* Association in the Ludlow of the Welsh Borderland does not represent an intrinsic position along an environmental gradient, and is interpreted as a single interruption of normal community development during progradation of proximal shelf deposits.

Environmental significance of the association

The environmental relations of the *S. ornatella* Association are best approached by considering those factors which do not appear to differentiate it from stratigraphically adjacent communities. These include the following.

1. Temperature, salinity, oxygen level. The broad faunal composition of the association clearly indicates that these factors could not have differed appreciably from other parts of the Ludlow sequence.
2. Bottom type. Grain size and composition are identical to sediment bearing different communities above and below.
3. Sedimentation conditions. An alternation of storm-deposited laminated beds and bioturbated siltstone is identical to other parts of the coquinoid siltstone facies bearing other communities.
4. Water depth. Following the sedimentary observations, it is very unlikely that depth of water over the Ludlow shelf changed significantly during Upper Leintwardine times.

5. Food supply. There is no evidence in acritarch abundance (Lister 1970) or size of benthic individuals to suggest any change in this factor.

After eliminating these factors, and considering that the *S. ornatella* Association is in part a reversion to the distal shelf fauna of the *M. laevigata* Association, a model involving larval dispersal may be proposed. Thorson (1950) observed that *Macoma* and *Syndosmya* communities of one part of the present inshore Danish waters are consistently recruited from larvae derived from a specific area tens of kilometres away, and not from larvae produced by local benthic populations. This is because of the prevailing current system, which disperses larvae from populations in one specific region to maintain bottom communities in another area.

From these observations, we may propose a temporary shelf-wide change in current system over the Welsh Borderland in Upper Leintwardine times. A change in current system could have carried larvae from distal shelf communities such as the *M. laevigata* Association to proximal shelf environments represented in the Upper Leintwardine Beds. These larvae, settling in a foreign environment, would produce an anomalous bottom community as long as these particular conditions of currents remained in effect.

There is no evidence for the location of the distal shelf environments which could have supplied larvae to areas where the *S. ornatella* Association is found. However, several faunal features of the *S. ornatella* Association conform with the model.

1. Brief, stratigraphically and ecologically disjunct occurrence of several species 'exotic' to the proximal shelf environment, such as *Isorthis clivosa* and *Mytilarca siluriana.*
2. Faunal dominance by leptaenids, *Shaleria* and *Atrypa*, which otherwise were of very low abundance and probably at the extremes of their tolerance limits in the coquinoid siltstone facies.
3. The addition of the exotic forms to the normal proximal shelf fauna rather than replacement (although substitution of *I. clivosa* for *I. orbicularis* is a notable exception).
4. The sudden appearance in the Upper Leintwardine Beds in both basin and shelf of species which are completely unknown in older strata (Lawson & Straw 1956). *Neobeyrichia lauensis* (Kiesow) and *Encrinurus stubblefieldi* are among these invaders.

The model is also supported by ecological aspects of graptolite distributions. In sections east of Ludlow, graptolites are extremely rare in the Bringewood Beds and Lower Leintwardine Beds and absent in the Whitcliffe Beds. They can be readily found with the *S. ornatella* Association in the Upper Leintwardine Beds, however – a monospecific assemblage of *Saetograptus leintwardinensis* (Lapworth). Surface currents carrying offshore larvae to proximal parts of the shelf would also carry plankton further inshore than usual. This would explain the very brief Upper Leintwardine incursion of graptolites over the shelf areas.

Synchrony and type section of the Upper Leintwardine Beds

If the model presented above is applicable, as suggested by several lines of evidence, then the *S. ornatella* Association must represent a synchronous ecological event. The synchrony of the Upper Leintwardine fauna has been accepted by Lawson & Straw (1956) and subsequent workers on the empirical basis of its short vertical range, wide geographic extent and inclusion of species new to the Welsh Basin.

In the type section of the Upper Leintwardine Beds, Holland *et al.* (1963 : 134) defined the base of this division as at the first occurrence of *Aegiria grayi*, *Calymene neointermedia* and *Encrinurus* sp. (now *E. stubblefieldi* Tripp). The type section has been sampled again here as section 2C, shown in Fig. 16. This sampling indicates that the base of the *S. ornatella* Association, as well as the incoming of common graptolites, occurs 2 m below the base of the Upper Leintwardine Beds as defined by Holland *et al.* (1963). The identity of the Upper Leintwardine Beds in shelf areas east of Ludlow has been established in this study and by Holland *et al.* (1963) on the basis of its whole faunal content, that is, the *Shaleria ornatella* Association. *Aegiria grayi* does not occur east of Ludlow (Holland & Lawson 1963), and the two trilobites are too rare to be consistently used for defining the base of the Upper Leintwardine Beds outside the type section.

The only practicable basis for identifying the base of the Upper Leintwardine Beds in the Welsh Borderland is the appearance of the whole *S. ornatella* Association. Correlations made on this basis do not correspond to the boundary of the Upper and Lower Leintwardine Beds as defined, but relate to a horizon 2 m lower in the type section. In practical terms of correlation, these upper 2 m of the type Lower Leintwardine Beds are of 'Upper Leintwardine' age.

Protochonetes ludloviensis Association

The *P. ludloviensis* Association is restricted to the coquinoid siltstone facies of the Whitcliffe Beds. It is a low-diversity community dominated by brachiopods and bivalves, and Pl. 5, figs 2–4 show representative assemblages of species. Faunal profiles of the association are shown in Figs 11, 16–18 and 20, and checklists of species are given in Appendix 3, Tables 16 and 20.

Brachiopods

Brachiopods comprise 82% of individuals collected from disturbed neighbourhood assemblages. *Protochonetes ludloviensis*, *Salopina lunata* and '*Camarotoechia*' *nucula* are the dominant species, and each may form as much as 80% of the fauna in single samples. *Howellella elegans* is also very abundant in the uppermost Whitcliffe Beds at Ludlow (Holland *et al.* 1963). Nine of the remaining 11 brachiopod species recorded from the association are extremely rare, and appear only sporadically in stratigraphic profiles. These, listed in Appendix 3, are survivors from the *S. ornatella* and *S. wilsoni* Associations, and were probably at the extreme of their environmental tolerance.

Protochonetes, *Salopina* and '*Camarotoechia*' show extreme small-scale fluctuations in abundance in stratigraphic sections (Figs 16–18 and 20). This corresponds to an unpredictable 'opportunistic' strategy of reproduction, as discussed for the upper phase of the *S. wilsoni* Association. As single assemblages, any brachiopod sample in the Whitcliffe Beds can be duplicated within the many faunal combinations shown in stratigraphic profiles of the upper phase of the *S. wilsoni* Association. The brachiopods of the *P. ludloviensis* Association are not new community elements, but simply a selection of the high diversity of species within the *S. wilsoni* Association.

Bivalves

Bivalves comprise 10% of all individuals collected from disturbed neighbourhood assemblages, but locally reach 30% of the fauna. Although they have not been observed to exceed brachiopods in number of specimens, they would often have exceeded brachiopods in biomass. Unlike brachiopods, bivalves of the association show no reduction in diversity relative to preceding communities, and 16 species have been recorded.

The endobyssate *Sedgwickia amygdalina* comprises 42% of total bivalve individuals. Other common species are *Goniophora cymbaeformis*, *Ptychopteria tenuistriata*, *Pteronitella retroflexa* and *Nuculites antiqua*. These species appear to show stratigraphic fluctuations in abundance similar to those of brachiopods (Tables 24 and 29), but sampling has not been extensive enough to document this fully.

Minor groups

Bryozoa consist almost wholly of ramose forms, and Owen (in Holland *et al.* 1963) listed three species from the Whitcliffe Beds at Ludlow, derived from the *P. ludloviensis* Association. Gastropods are present in low abundance, and represented mainly by *Bucanopsis expansus* and *Cyclonema corallii*. Cephalopods of probable nektobenthic habit are fairly continuously present (Fig. 17).

Ostracods have a sporadic and occasionally dense occurrence like those of the upper phase of the *S. wilsoni* Association. Rare trilobites are *Acastella spinosa* and *Homalonotus knightii*; *E. stubblefieldi* survives into the basal few metres of the association at Ludlow. Telson parts of the crustacean *Ceratiocaris* comprise 0·1% of the collected fauna, and whole individuals, exceeding 20 cm in length, were described by Jones & Woodward (1888–89). Kjellesvig-Waering (1961) discussed the eurypterid fauna at the stratigraphic horizon occupied by the *P. ludloviensis* Association. One eurypterid fragment, representing less than 0·1 % of the collected fauna, was found in this study.

Crinoid columnals less than 2 mm in diameter occur in low density throughout bioturbated sediment, and occasionally are concentrated in transported shell layers. Ramsbottom (1958) recorded whole individuals of the crinoid *Cicerocrinus elegans* Sollas from the Whitcliffe at Ludlow, but gave no information to indicate whether they were from the Whitcliffe Beds or Leintwardine Beds. Allen & Tarlo (1963) recorded a low-diversity marine fish fauna in the Whitcliffe Beds.

Environmental relations of the association

In overall stratigraphic pattern, the *Protochonetes ludloviensis* Association is a restriction of previous faunas of the Leintwardine Beds rather than a 'new' community of replacing species appearing along an environmental gradient. This can be seen in the Woodbury Quarry section (Fig. 17). The *P. ludloviensis* Association is marked by significant reductions in diversity of brachiopods and bryozoa, but no reductions occur in bivalves. This suggests an increase in sedimentation rate, adversely affecting epifaunal lophophorate groups, but not affecting infauna. Sedimentary features in the coquinoid siltstone facies of the Whitcliffe Beds, described above (p. 189), indicate the highest relative sedimentation rates in the Ludlow shelf sequence. However, the *P. ludloviensis* Association appears in sections at Ludlow and Perton within an extensive interval of bioturbated sediment, before these features become common (Figs 16 and 20).

Relation of the association to Downtonian faunas

The upper stratigraphic boundary of the *P. ludloviensis* Association has been studied at Ludlow, where the final occurrence of the community is shown at the top of section 2A in Fig. 16. In this section, assemblages dominated by *Protochonetes*, *Salopina* and '*Camarotoechia*' occur up to the base of the Ludlow Bone Bed, with no reduction in species or general faunal change.

The Ludlow Bone Bed grades from a single bed of bone material, several cm thick at locality 7 of Holland *et al.* (1963), to two or more separate horizons of bone material 1 cm or less thick in section 2A of this report. This transition occurs over a lateral distance of about 100 m. The separate thinner bone layers are shown in Pl. 3, fig. 1; they have sharp, erosional bases and are overlain by parallel-laminated siltstone. The sedimentary features and lateral impersistence of the Ludlow Bone Bed are identical to shell beds interpreted earlier as rapid storm deposits. They do not indicate a slow in-place accumulation of the bone material.

The invertebrate fauna within the Ludlow Bone Bed and associated parallel-laminated siltstone is shown as the stratigraphically highest sample in Fig. 16. It is a typical transported assemblage of the *P. ludloviensis* Association, impoverished in infaunal bivalves. The *P. ludloviensis* Association completely disappears above the bone bed. This disappearance is correlated with other biological events. *Chondrites* and associated deformative bioturbation are present immediately below the Ludlow Bone Bed, but were not observed in strata above. Acritarchs dominate the microflora below the Ludlow Bone Bed, but are very rapidly replaced by spores of land plant type in beds above (Richardson & Lister 1969). These biological disappearances correspond to both an environmental and a temporal non-sequence. The sedimentary evidence indicates that the non-sequence is not represented within the bone bed, but at an erosional surface at its base.

The Downtonian fauna above the Ludlow Bone Bed consists of fish, eurypterids, molluscs, lingulids and ostracods. This brackish-water community occurs throughout the Welsh Borderland, and shows low species diversity and a very sporadic pattern of occurrence. The fish and eurypterid faunas are taxonomically distinct from those in the marine upper Ludlow deposits (Kjellesvig-Waering 1961; Allen & Tarlo 1963). Dominant invertebrates are *Modiolopsis complanata* (J. de C. Sowerby), *Platychisma helicites* (J. de C. Sowerby) and *Lingula cornea* (J. de C. Sowerby). Any of these species may form 100 % of local assemblages.

The stratigraphic pattern of Ludlow communities

Discreteness and number of communities

Ludlow communities in the study area have been defined by distinctive overlaps in stratigraphic ranges and relative abundances of a complex of benthic invertebrates. The ranges and abundance changes occur along a sedimentary-environmental gradient preserved in stratigraphic sections, and for the most part reflect ecological phenomena rather than evolutionary events. Inspection of faunal profiles such as Figs 17 and 18 will show that species ranges form a finite number of distinctive overlaps, described as 'Associations', along the stratigraphic transect of depositional environments. Ludlow communities are intergrading, as discussed below, but the intergradation is not so complete that any arbitrary number of communities can be recognized. The presence of only a few 'natural' faunal divisions within the Ludlow of the Welsh Borderland is also implicit in the work of Holland *et al.* (1963) and Lawson (1975).

The relative stratigraphic discreteness of Ludlow shelf communities results from an interplay of two types of faunal patterns in measured sections. One pattern consists of temporal variation within an association, where sediments do not change, species composition remains relatively constant, but relative abundances of species fluctuate. This pattern represents faunal variation during the persistence of constant major environmental conditions. In the second type of faunal pattern, directional stratigraphic changes occur in the species present, with appearances, disappearances and shifts in relative abundances which do not return to any previous state. This type of pattern represents the stratigraphic gradation from one association to another, and is usually accompanied by a change in sedimentary facies. With the exception of the transition between the *G. obovata* and *M. laevigata* Associations, the gradations occupy thicknesses of strata much subordinate to those occupied by faunas showing the first type of pattern. It is this subordinate stratigraphic nature of faunal gradations that lends a discreteness and finite number to the associations defined in measured sections.

Boundaries between communities

The conclusions reached here on the discreteness of Ludlow communities may appear, at first sight, to be in conflict with those of Calef & Hancock (1974), who stated that Ludlow communities of the Welsh Borderland were continuously intergrading in faunal content. This statement was correct for their available data, which was derived from about 50 spot samples embracing most of the area shown in Fig. 1, p. 177. If only the average content of the associations recognized here is compared, they can indeed be considered as completely intergrading in properties such as diversity, abundance of certain forms, etc. Some of these general trends will be discussed later.

When considered by continuous stratigraphic profiles, however, boundaries between Ludlow communities emerge, in which major ecological changes in fauna can be located in a definite and often restricted interval of strata. These boundaries range from the 30 to 50 m gradational interval between the *G. obovata* Association and *M. laevigata* Association to the contacts of the *S. ornatella* Association, which can be located within a metre of strata or less. Variation in scale and other properties of boundaries reveal aspects of Ludlow communities which are not apparent in considering average content.

Most stratigraphic boundaries between Ludlow communities are marked by immigration of species into the depositional area. This may occur at the boundary in question, or some distance below it, with the actual boundary of communities showing an increase in relative abundance of the immigrants. Disappearances of species from the previous community also occur within or near the boundary interval, and changes in relative abundance may occur among forms which range between communities. The faunal changes at boundaries tend to occur among forms in a particular rank order, in the general fashion predicted by Johnson (1972). Some of these rank orders have been described above, pages 224 and 228.

Where the faunal changes occur through an extensive interval of strata, as between the *G. obovata* and *M. laevigata* Associations, we may postulate a very slow change in environment. This is corroborated by the gradual transition, in this interval, from the mudstone facies to overlying sediments. The boundary between the *M. laevigata* and *S. wilsoni* Associations, as seen near Ludlow (Fig. 16), also consists of an alteration in fauna, but occupies only about 2 m of strata. Here environmental changes appear to have occurred relatively quickly. The sharpest stratigraphic boundaries are those of the *S. ornatella* Association, which can be located within centimetres. It is significant, in this regard, that the *S. ornatella* Association appears to represent a hydrographical event, and not a change in bottom sedimentation.

A second type of boundary between Ludlow communities does not involve the arrival of immigrants, but is marked only by disappearances of forms and shifts in relative abundances. Such boundaries are seen at the bases of the *A. reticularis* – coral Association and *P. ludloviensis* Association, and result in a lowering of species diversity. Rollins & Donahue (1975) related this type of phenomenon to an increase in physiological stress upon organisms. It results in the formation of a 'relict' community from elements of a previously more diverse community.

The Ludlow community pattern as a product of environmental histories

Johnson (1972) has discussed how the discreteness of benthic communities varies according to the nature of environmental gradients. Sharp environmental breaks result in discrete benthic communities and intergrading environments result in extensive gradations between communities. In stratigraphic sections, the rate of environmental change is an important analogy to this situation. The apparent discreteness of most Ludlow communities can be related to long-term persistence of certain environmental conditions, alternating with more rapid intervals of environmental change.

One category of environmental change relates to the major stratigraphic patterns of terrigenous sedimentation, which were summarized in the sedimentology section, p. 192. Each of the three major terrigenous facies persists for several tens of metres before grading into a succeeding facies within a smaller stratigraphic thickness. This supports the concept that intervals of environmental change in the Welsh Borderland, producing community boundaries, were temporally subordinate to times of environmental constancy. The vertical sequence of communities found in the major terrigenous facies (in ascending order, the *G. obovata*, *M. laevigata*, *S. wilsoni* and *P. ludloviensis* Associations) represents the superposition of a normal lateral community sequence.

A second category of environmental change producing relatively discrete community boundaries in the Ludlow sections appears to be caused by temporary hydrographic anomalies in the depositional area. The *Atrypa reticularis* – coral Association is related to interruption of terrigenous depositional patterns by restricted circulation and back-barrier, carbonate muds. The *Shaleria ornatella* Association can be related to a change in current patterns affecting larval dispersal. Neither association relates to the terrigenous environmental gradient which affected other shelf communites. Instead, they represent unique temporal interruptions of this community sequence.

Both the number and level of discreteness of Ludlow communities in the study area are products of the history of the environments represented in stratigraphic sections. They appear to relate to the nature and rate of terrigenous progradation over the Welsh Borderland shelf, as well as to temporary hydrographic anomalies. The observed faunal patterns are almost certainly not a reflection of any intrinsic biological discreteness of Upper Silurian benthic communities. The same forms of life as those in the Ludlow shelf sections would probably show a different pattern of community number and discreteness in an area with a different environmental history.

Trends in species diversity

The stability-time hypothesis

Sanders (1968) proposed the stability-time hypothesis to explain diversity differences between two abstract types of marine communities.

1. 'Physically-controlled community' – Small numbers of eurytopic species, adapted primarily to the physical environment, are present. Physical conditions expose organisms to severe physiological stress, and fluctuate widely.
2. 'Biologically-accommodated community' – Large numbers of stenotopic species are

present, forming stable, complex associations developed through a history of biological interaction. Physical conditions are fairly uniform and constant through time.

Sanders (1968) stated that biologically-accommodated communities will grade into physically-controlled communities along an environmental gradient of increasing physiological stress. This gradient may be expressed across either space or time, and will involve an increase in species diversity with increasing environmental stress. Slobodkin & Sanders (1969) stated that unpredictable fluctuations in the physical environment will be a greater cause of physiological stress to organisms than predictable fluctuations.

Ludlow stratigraphic sections as an environmental stress gradient

The terrigenous sedimentary facies in Ludlow shelf sections represent a gradient of increasing environmental stress upon bottom faunas. Sedimentary conditions were most stable in the mudstone facies at the distal shelf end of the gradient. This is indicated by extreme uniformity of sediment, complete bioturbation and rarity of current-deposited beds. More variable sedimentation began in the succeeding bioturbated siltstone facies, with the introduction of minor erosion and sporadic distal deposition of laminated silt sheets. The proximal shelf coquinoid siltstone facies, at the top of Ludlow sections, represents the high-stress end of this environmental gradient. Decrease in bioturbation, frequent erosional surfaces, transported shell beds and frequent storm-deposited laminated silts in this facies show fluctuating patterns of deposition and very high local rates of sedimentation.

Faunal destructions caused by storm sedimentation may be considered a primary cause of biologically-directed stress in the Ludlow shelf environments. The frequency of storm-sedimentation events, as well as their probable intensity, increases stratigraphically from the mudstone facies to the coquinoid siltstone facies. Faunal destructions by bentonite deposition represents another type of biologically-directed stress. This type of event, however, was less prevalent than storm sedimentation, and distributed fairly equally across the shelf environments.

Diversity gradients in Ludlow communities

Indices of species diversity in communities of the major terrigenous facies are given in Table 13.

Table 13 Diversity indices for communities of the major Ludlow sedimentary facies. *The indices give the mean number of species at a sample of 50 individuals, based on the rarefaction method of Sanders (1968). Go – *G. obovata* Association; tran – transitional fauna between *G. obovata* and *M. laevigata* Associations; Ml – *M. laevigata* Association; lpSw – lower phase of *S. wilsoni* Association; upSw – upper phase of *S. wilsoni* Association; Pl – *P. ludloviensis* Association

stratigraphic unit	Elton Beds		Bringewood Beds		Leintwardine and Whitcliffe Beds	
facies	mudstone		bioturbated siltstone		coquinoid siltstone	
number of samples	(35)	(11)	(61)	(21)	(28)	(44)
association	Go	tran	Ml	lpSw	upSw	Pl
mean diversity per sample*	10·9	16·0	14·2	11·4	9·7	8·0

Average diversity values of the communities show a continuous decrease from the 'transition fauna' of the Upper Elton Beds to the *P. ludloviensis* Association of the Whitcliffe Beds. This decrease in diversity follows predictions of the stability-time hypothesis, and appears to be directly related to the increasing sedimentation-produced stress in the depositional environments. Stratigraphic plots of diversity by single sample show that this trend includes many small fluctuations on a metre-by-metre basis (Fig. 17). Although the overall decrease in diversity correlates with the pattern of sedimentary stress, species diversity at any particular point along the gradient appears to have been subject to second-order influences.

The *Glassia obovata* Association of the mudstone facies is an exception to the diversity trend. Although present in a distal shelf quiet-water environment with probably the slowest and most uniform sedimentation rate, it does not have the highest diversity of the Ludlow communities (Table 13). Softness of the muddy substrate, discussed on p. 222), may have limited the community to a particular diversity of specialized taxa, in spite of low-stress sedimentation conditions.

Biological accommodation

Although the broad diversity trend in Ludlow communities corresponds to predictions of the stability-time hypothesis regarding the effects of environmental stress, it is unlikely that diverse communities in the distal shelf environments of low sedimentation rate were truly biologically accommodated. If biological accommodation, resulting from a history of organism interactions, is a progressive process, we would expect to see diversity increases in communities with long persistence in a low-stress environment (Sanders & Hessler 1969). The *Mesopholidostrophia laevigata* Association is one of the most diverse Ludlow communities, and has been sampled through 60 m of constant bioturbated siltstone facies in Woodbury Quarry (Fig. 17). Although probably hundreds of thousands of years are represented by these strata, the association shows no increase in diversity. Instead, a general stability in diversity is seen, with values throughout the 60 m interval varying about a mean of 14–15 species per 50-individual sample size. Similar stable levels of diversity during temporal persistence of distal shelf conditions can be seen in Figs 5, 19 and 22. We will return to the topic of biological accommodation in the concluding discussion of Silurian benthic communities.

A stratigraphic consideration of opportunistic species

The numerical decline in species diversity within Ludlow communities in high stress sedimentary environments is directly related to the extreme dominance of samples by individuals of a single species. 'Opportunistic' species are those which are capable of rapid and temporary expansion in population size (MacArthur 1960). Many Ludlow species appear suddenly in great abundance and then wane or disappear over distances of centimetres or less in stratigraphic sections, particularly within the high-stress environment represented by the coquinoid siltstone facies. Hallam (1972 : figs 4–8) proposed a simple model which relates this type of stratigraphic phenomenon to MacArthur's concept of opportunism. According to Hallam's model, opportunistic species can be distinguished by great abundances of individuals which persist over only short stratigraphic distances. In contrast, Hallam (1972) proposed that 'equilibrium species' would be distinguished by a constant presence through stratigraphic sections without isolated peaks of extremely great abundance.

Hallam's model can be applied to Ludlow sections by the quantitative treatment of stratigraphic persistence of species and their relative abundance. We shall define Y as the maximum relative abundance a species reaches in any single sample. This indicates its maximum reproductive potential, relative to other species. X will be defined as the maximum number of continuous records of a species in samples taken at 1 m intervals along a stratigraphic section. This is a measure of its temporal persistence at a given depositional site. Note than low Y values for a species will normally bias its record toward low X values, as discussed in Appendix 2, p. 261.

Only certain of the Ludlow communities occupy stratigraphic intervals large enough to permit the use of this method, and only brachiopods are sufficiently numerous to lend themselves to the quantitative treatment. Plots of brachiopod species in the XY field, by community, are shown in Fig. 24. Species with plots falling in the upper left corner of the field, with high Y values (reproductive potential) and low X values (temporal constancy) can be considered as opportunistic. It is apparent that there is a gradation, rather than any natural breaks, in the positions into which various species fall when plotted within the field. An arbitrary line, drawn around the upper left corner of the XY field (Fig. 24), allows a consistent numerical definition of an 'opportunistic species', and permits relative comparisons to be made of the percentages of such species between different Ludlow communities.

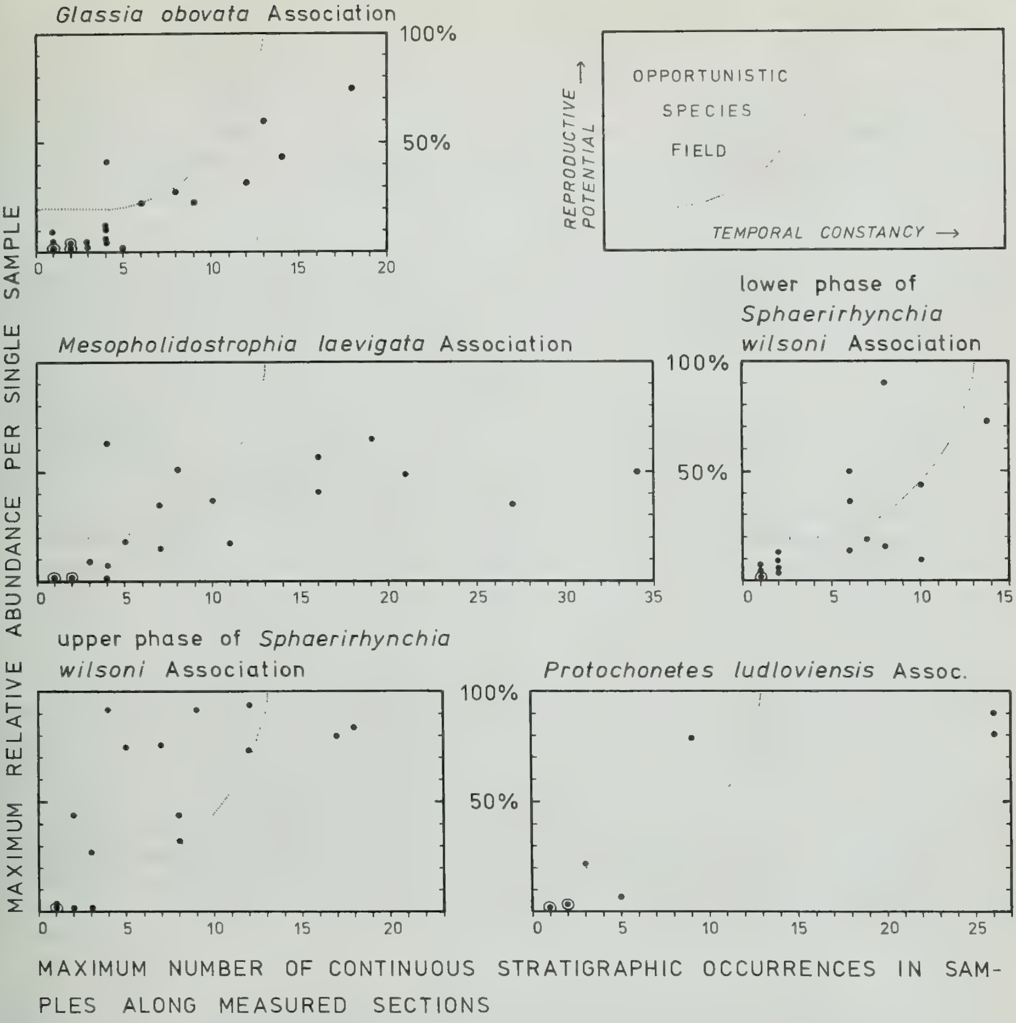

Fig. 24 Definition and comparison of opportunistic species in Ludlow communities. Dots represent values for single brachiopod species, and dots with circles represent several species. The 'opportunistic species field' is defined to include the major cluster of species in the upper phase of the *Sphaerirhynchia wilsoni* Association. This provides a method for making relative comparisons of opportunism between communities. Sources of bias in the plots and further discussion are given in the text.

Table 14 summarizes the *XY* plots in Fig. 24 according to the percentage of arbitrarily-defined opportunistic brachiopod species within Ludlow communities. The lowest percentage of opportunistic species is present in the *G. obovata* Association of the mudstone facies. Percentage of opportunists increase in communities of the stratigraphically higher bioturbated siltstone facies, and the highest percentage of opportunism occurs in the *S. wilsoni* Association of the coquinoid siltstone facies. Table 14 shows that, in general, the increase in environmental sedimentation-produced stress in Ludlow stratigraphic sections is accompanied by increased percentages within communities of brachiopod species with opportunistic patterns of occurrence.

Hallam (1972) also suggested that eurytopic species may change their population strategies over their environmental range. This is shown by several Ludlow brachiopods. *Isorthis*, for example, has plots as an 'equilibrium species' in communities of the bioturbated siltstone facies, but as an 'opportunistic species' in the *S. wilsoni* Association of the coquinoid siltstone facies.

The *P. ludloviensis* Association, at the most high-stress end of the stratigraphic-environmental gradient, is an apparent anomaly in the trend discussed above (Table 14). This is because most of its recorded brachiopod species are very rare survivors from previous communities. These species have plots in the lower left corner of the *XY* field (Fig. 24), and bias the calculation of opportunism within the association.

Table 14 Percentages of opportunistic brachiopod species in Ludlow communities, as determined by criteria in Fig. 24, p. 243. Go – *G. obovata* Association; Ml – *M. laevigata* Association; lpSw – lower phase of *S. wilsoni* Association; upSw – upper phase of *S. wilsoni* Association; Pl – *P. ludloviensis* Association

stratigraphic unit	Elton Beds	Bringewood Beds		Leintwardine and Whitcliffe Beds	
facies	mudstone	bioturbated siltstone		coquinoid siltstone	
association	Go	Ml	lpSw	upSw	Pl
number of brachiopod species	30	32	27	19	15
percent opportunistic species	3	9	11	53	13

The trends in opportunism within Ludlow communities correlate with observed features of the major terrigenous sedimentary facies, which suggests a direct relation to sedimentation-produced environmental stress. Susceptibility of populations to total destruction during storm-sedimentation events was probably a factor which favoured opportunistic reproductive strategies among Ludlow brachiopods, as discussed above, p. 231. Alternative explanations for the opportunistic patterns, not directly observable in the rock record, may also be involved. For example, fluctuating levels of food resources may contribute to dominance of marine communities by opportunistic species, and stable, and often lower, levels of resources may favour equilibrium species (Valentine 1971). Patterns of predation may also affect numerical fluctuations of particular species, as discussed later.

Faunal destructions in Ludlow communities

Bentonites and storm-deposited silts

As noted earlier, bentonites and storm-deposited sheets of laminated silt represent two types of biologically-destructive events preserved in Ludlow sections. Frequency of the later type of event shows a general correlation with decreased diversity of fauna and abundance of opportunistic species, as we have seen. In this section, we wish to test whether these events have any specific effect on the small-scale stratigraphic variation within particular communities.

Bentonites contain no burrows or body fossils, and extend laterally for great lengths along Ludlow outcrops. They were probably formed by rapid ashfalls, killing the benthic faunas on which they settled. Shells immediately below a bentonite are usually widely scattered and variably orientated, as elsewhere in bioturbated sediment. Storm-deposited laminated sheets of silt also rapidly buried and destroyed benthic faunas at particular sites. Concentration of epifaunal shells at the base of these sheets, burial of infaunal shells below them, and lack of escape trails indicate this total destruction. By analogy with modern processes, these destructive events were probably of very short duration, occurring over a day or less. Bentonites and storm-deposited silts are overlain by fossiliferous bioturbated sediment, indicating a return of normal, slow sedimentation following ashfalls or storms, and recolonization of the new sediment by benthos.

A model of recolonization

Ecological succession is a process by which a community at a particular place changes predictably in composition through time, either through change in physical environment, the effects of biotic activity of organisms, or both. Johnson (1972) proposed that succession is an integral part of marine benthic communities, and has developed a predictive model around this concept. Following theoretical considerations by Margalef (1968), Johnson's model states that a benthic community can exist in either an immature, early stage of succession, or later, mature stages of succession, which develop in an orderly, predictable fashion from the former state. Destructive physical disturbances of the environment will downgrade a community to its earliest successional state, following which it can gradually return to maturity through processes involving an increase in species diversity, increase in inert organic matter and biogenic structures, and decrease in fluctuations of population size. Stratigraphic sections of sediments with repeated environmental disturbances should contain communities showing repetitive successional events, each beginning with a downgrading following a disturbance.

Johnson (1972 : 155) considered the way succession would proceed when organisms recolonize a bottom following destructive events such as ashfall or storm-sedimentation.

> A newly deposited sediment is a relatively homogeneous habitat. As organic detritus accumulates at the sediment-water interface, the animals rework it into the underlying sediment. Through their feeding and burrowing activities, the sediment becomes increasingly heterogeneous on a small scale. The particle size, composition, and stability of the sediment may be altered . . . In addition, the activities of micro-organisms must profoundly affect the chemical environment. The accumulation of shells and burrows would further add to the heterogeneity of the infaunal environment . . . These modifications of the sediment must be accompanied by faunal changes. We would expect that the attractiveness of the substrate to settling larvae would change . . . In the beginning, species diversity would be low in the relatively homogeneous sediment. As the sediment becomes progressively more heterogeneous, providing more microhabitats, diversity should rise.

Comparison of the model with Ludlow faunal profiles

Fig. 25 shows a small-scale vertical profile of the *M. laevigata* Association which is interrupted by two bentonite beds. From this profile, we may note the following.

1. Density of shells per surface area of sediment immediately above the bentonites is in one case the same, and in one case higher than immediately below bentonites and in other parts of the section.
2. Species diversity immediately above both bentonites is not lower than in other parts of the section.
3. Species content immediately above a bentonite does not differ from that immediately below, either in the species present or the relative abundance of their individuals. The two bentonites do not divide the faunal profile into two repetitive faunal cycles.

The small-scale example shown in Fig. 25 is a detail of the larger faunal profile for the Woodbury Quarry section (Fig. 17). Again, in the larger section, there is no evidence of repetitive cyclical development of diversity and faunal patterns relating to bentonites. This same relation is seen in several other sections, shown in Figs 16, 21, 22 and 23. Storm-deposited beds of siltstone also appear to have no downgrading effect upon Ludlow communities. In Fig. 10, for example, note that sample 4A37, immediately above a storm-silt bed, does not show lower species diversity than samples 4A39, 4A40 and 4A42, which were taken from bioturbated sediment several centimetres above such storm-silts.

It is not possible to detect any downgrading or repetitive succession in Ludlow communities caused by bentonites or storm-deposited silts. The sedimentary record above such beds indicates an apparent immediate recolonization by the same species, often with the same quantitative proportions of individuals, as existed before the destructive event. However, some initial biotic conditioning of sediment, as discussed by Johnson (1972), must have preceded this recolonization. Rates of reworking by macrofaunal burrowers could produce substantial modifications of the sediment within days (Rhoads 1963), and chemical changes caused by micro-organisms may be as rapid. If a succession from micro-organisms to macro-burrowers to epifaunal assemblages can occur within days or weeks, it would probably be undetectable in a stratigraphic section. The key aspect of this problem is rate of shelf sedimentation. Apart from storm events, sedimentation rate on the Ludlow shelf was probably much slower than the time required for a sediment-conditioning type of succession. If such sediment-conditioning affected the order of arrival of shelled colonists, slow sedimentation rate would insure that virtually all successive arrivals were preserved in the same few millimetres of strata.

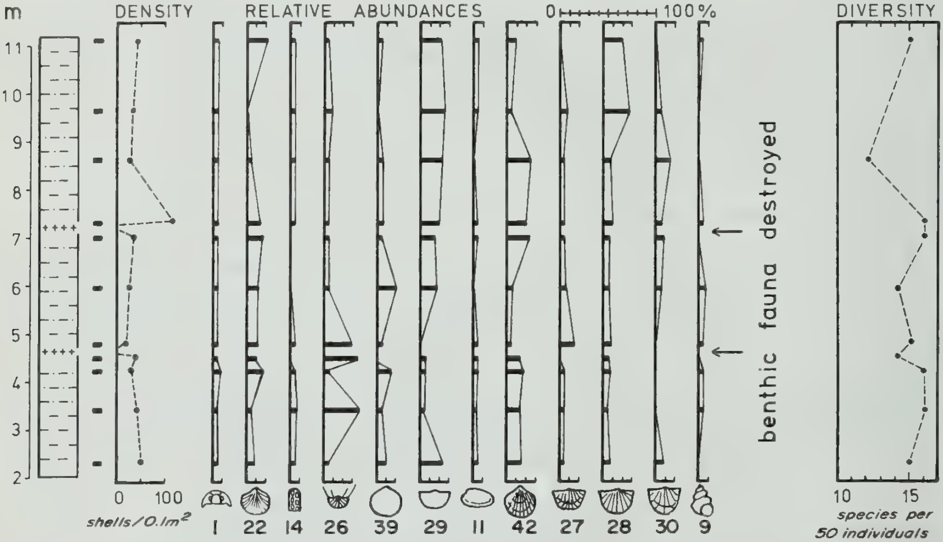

Fig. 25 Detail of the *Mesopholidostrophia laevigata* Association in section 3A, Lower Bringewood Beds, Woodbury Quarry. Note the lack of relation of faunal patterns and the diversity curve to the two intervals of faunal destruction. Metre readings locate this profile in the larger section shown in Fig. 17. Lithological and faunal symbols are explained in Figs 14 and 15.

Stratigraphic variation within communities

Variation within distal *versus* proximal shelf environments

As discussed in a previous section (p. 239), a basic identity is given to each of the Ludlow associations by a stratigraphic interval in which species content remains generally the same, and relative abundances of most species fluctuate back and forth. This pattern represents variation within a community during the relatively long-term persistence of certain major environmental conditions. In the proximal shelf, coquinoid siltstone facies, variations in relative abundances are extreme, and occur unpredictably in stratigraphic sections, literally centimetre by centimetre. This has been related to opportunistic strategies of reproduction in the dominant species within this environment. A contrasting pattern is seen in the mudstone facies and bioturbated siltstone facies, which represent distal shelf environments of lower physiologic stress. Here, many brachiopod species of the *G. obovata* and *M. laevigata* Associations show gradual stratigraphic cycles in abundance, in which the relative abundance of a species in any particular sample can generally be predicted from information on its abundance in samples above and below. These fluctuations occupy several metres of strata, and may relate to time spans of hundreds or thousands of years. They are not related to bentonites, as will be discussed later, and occur within very uniform bioturbated silt and clay.

Johnson's model of succession

Johnson (1972 : 152) has expressed this problem as follows.

> We do observe changes in species composition in modern communities without any noticeable change in the overall physical environment. Similarly, we commonly observe changes in continuous stratigraphic sequences that are not accompanied by any obvious change in lithology. Some of these may be the result of the vagaries of recruitment. More often such faunal changes probably are the result of the ecological interactions involved in succession.

Although Johnson's concept of succession has been shown to be inapplicable to the preserved faunal record relative to Ludlow bentonites and storm-silt beds, it must still be tested against those fluctuations which do occur in Ludlow communities. According to the model, successions seen in stratigraphic sections would involve faunal repetitions, each consisting of an ordered serial set of successional stages. Following some type of environmental disturbance, the community at a particular site would be downgraded to its earliest serial stage of succession. According to Johnson (1972) and Walker & Alberstadt (1975), this stage would be characterized by low species diversity, and dominated by a small number of those species of the community which are most eurytopic, or capable of existing outside the community's habitat. If the disturbing event does not persist, and the environment returns to some optimal condition, the model states that the community would undergo succession through progressively more mature stages, eventually reaching some sort of climax and equilibrium state. Walker & Alberstadt (1975 : fig. 1) have indicated some of the expected events in such a succession. For our purposes, the two most important are an increase in species diversity and an increased representation of 'characteristic species', that is, relatively stenotopic forms which are generally restricted to the particular community in question.

We will compare this model with the stratigraphic profile of the *M. laevigata* Association in Woodbury Quarry (Fig. 17), which shows many fluctuations in brachiopod species involving the regular increases and decreases in relative abundance of each species described earlier. The critical point is whether the stratigraphic fluctuations of each species relate to one another in the ordered, repetitive manner predicted by the model.

First, consider some 'characteristic species', restricted wholly or mainly to the *M. laevigata* Association: *E. radiatus* (taxon 49 in Fig. 17), '*Schuchertella*' sp. (taxon 36), *S. euglypha* (taxon 30), *A. funiculata* (taxon 27), *M. laevigata* (taxon 29) and *L. filosa* (taxon 28). All show cyclical patterns of abundance in the stratigraphic section. Next, consider those species which are present in the *M. laevigata* Association, but also commonly occur in other communities ('ubiquitous' and 'intergrading' species of Johnson 1972): *D. hybrida* (taxon 20 of Fig. 17), *A. reticularis* (taxon 42), *Isorthis* (taxon 22) and *S. wilsoni* (taxon 39).

If the stratigraphic variation within the *M. laevigata* Association conformed to the model of succession, we would see the following repeated pattern: 1. A stage with low species diversity and high abundance of taxa 20, 22, 39 and 42; 2. Gradual increase in species diversity accompanied by appearance of the 'characteristic' taxa listed above; 3. An interval of highest diversity consisting mainly of equitable abundances of the 'characteristic' taxa; 4. A downgrading of the community to the first stage and repetition of the succession.

No such pattern is apparent in the faunal profile in Fig. 17. The 'intergrading' and 'ubiquitous' species in the *M. laevigata* Association do not reach maximum abundances which, according to the model, would precede the appearance of the 'characteristic' species. The 'characteristic' forms are not restricted to stratigraphic intervals of highest species diversity of the community. In summary, neither the specific faunal sequence nor the repetitive aspects predicted by the model are apparent in the *M. laevigata* Association of Woodbury Quarry (Fig. 17). A similar situation can be seen in other faunal profiles in Figs 19–22. The stratigraphic variations within the *M. laevigata* and *G. obovata* Associations are probably not the result of repetitive ecological succession.

A model of temporal variation in larval recruitment

In the quotation presented earlier, Johnson (1972) noted a second explanation for fluctuations in community composition within a stratigraphic section under the phrase 'vagaries of recruitment'.

Studies of the recruitment of modern shallow communities in Danish waters show less randomness in this process than might be supposed, and provide a basis for constructing a model to test in stratigraphic sections.

Coe (1957), Johnson (1970) and Parker (1975) showed that temporal variations occur in shallow marine communities over periods of several years with no observed correlative change in the environment. The most extensive series of observations documenting this phenomenon are those of Blegvad (1925, 1928), who monitored the composition of shallow communities in the Danish Limfjord between 1910 and 1927. Blegvad's data show that although the species composition at particular sites remained relatively constant over this period, the densities of individuals of each species (and thus, their relative abundance) varied considerably. During certain successive years, densities of particular species remained low, and in other successive years, densities increased to some highest value before falling. Graphic presentation of these data by Blegvad (1925, 1928) shows no evidence of repetitive ecological succession relating to the fluctuations of species. Blegvad (1928) found that fish predation affected the temporal pattern of the fluctuations, but noted no other influences of biotic interaction or benthic environmental change.

The number of planktic larvae in the water column was the major factor associated with the fluctuations in abundance of each species. Blegvad (1928) observed that times of high density of benthic individuals of a particular species correlated with maxima of its planktic larvae in the preceding spawning season, and that periods of low benthic density correlated with preceding paucity of planktic larvae. He also noted that the amount of planktic larvae of a species was not directly related to the density of reproducing benthic individuals. Spawning of low-density benthic populations could result in either low or high numbers of larvae found in the water column, etc.

Thorson's (1950) summary of larval development provided explanations for many of the empirical observations of Blegvad. Thorson (1950 : fig. 2) showed that temporal variations in species with long planktic larval lives were greater than in species with short larval lives or direct development. He noted that larvae spending several weeks in the water column are affected by a number of purely pelagic environmental factors. These include losses within the larval population because of predation, fluctuations in their food supply of phytoplankton and movement away from suitable settling areas by currents. Such factors can affect the recruitment of benthic populations in the absence of change within the bottom environment.

Two important aspects of the Danish studies form a model for evaluating stratigraphic profiles of fauna.

1. In the modern examples, fluctuation in larval settlement and consequent benthic densities is not random. Several successive years of low larval numbers and small benthic populations alternate with several successive years of high larval densities and larger benthic populations.
2. Discrete events in the bottom environment or the size or presence of benthic populations are not the only factors influencing larval recruitment. Environmental factors in the water column, and not the bottom environment, may form a first-order control on the size of the larval population available for settling.

Comparison of the larval model with Ludlow sections

Species fluctuations in stratigraphic profiles of the *M. laevigata* and *G. obovata* Associations conform with the larval model in showing a lack of relation to bentonites, which represent discrete disturbances of the bottom environment. Note the cycles of relative abundance shown by *Protochonetes minimus* (taxon 26) in Fig. 25. Between 4·5 and 6 m in the section, *P. minimus* shows a cycle of high abundance. A bentonite caused a faunal destruction within this interval, but did not affect the cycle, for *P. minimus* maintains a nearly equal, high abundance both below and above the bentonite. Between 6 and 11 m in the section (Fig. 25), *P. minimus* shows a constant, low abundance. A second bentonite in this interval also fails to affect the occurrence of the species, which retains an equal, low abundance both below and above. Identical relations can be seen for many other brachiopod species in Figs 17, 22 and 25. Definite cycles of high and low abundances of particular species in the stratigraphic sections are virtually independent of the stratigraphic position of the bentonites.

These relations show that the stratigraphic fluctuations of species are independent of discrete changes in the bottom environment. They also show that presence of benthic populations of adults was not a necessary prerequisite for the settling of larvae of a particular species at the same site. Abundant adult populations, smothered by bentonites 2–5 cm thick, are followed by abundant larval settlement above the bentonite, without the possibility of direct attractive influence of pre-bentonite populations upon post-bentonite settlement of larvae. The best explanation for these phenomena, provided by the modern model, is that stratigraphic fluctuations in Ludlow species were controlled primarily by pelagic influences on larval survival, and not by benthic populations or events.

Brachiopod species in Ludlow distal shelf facies show a general stratigraphic pattern in which several metres of low-abundance occurrences alternate with intervals of higher abundance. No repetitive or successional relation is seen between the fluctuations of one species and those of others. This compares closely with the temporal patterns in modern species observed by Blegvad (1925, 1928). An important point, however, is the difference in time scale between Blegvad's observations and the probably longer spans of species fluctuations in the Ludlow sections. Walker & Bambach (1971) have emphasized that untransported assemblages of shells in fine-grained sediment represent a 'time-averaged' sample of many generations of individuals which lived at the same site. The fluctuations observed by Blegvad occurred only over several years, and the total pattern he observed of high and low abundances over 17 years would probably be preserved as a single averaged assemblage in a few mm of slowly-deposited distal shelf sediment. In spite of time-averaging, the cumulative effect of the type of fluctuation observed by Blegvad could be expressed in a stratigraphic section if the net average of fluctuations over a period of several hundreds or thousands of years differed from the average in a succeeding long period of time.

The model of pelagically-controlled larval effects provides a better explanation for the stratigraphic variations within Ludlow distal shelf communities than a model of ecological succession within the bottom environment. The time-scale of fluctuations seen in the Ludlow communities is not comparable with that known in modern examples. It is proposed, however, that time-averaging of fossil assemblages would grossly preserve, rather than completely obscure, the larvally-related temporal variation known in modern communities.

Biotic interaction in Ludlow communities

Predation

The foregoing analysis of stratigraphic patterns in Ludlow communities has reached negative conclusions regarding the existence of ecological succession, which implies a lack of the type of organism interactions and feedback which are an integral part of succession (Margalef 1968). Limited evidence does exist, however, for some direct interaction in Ludlow communities. One type of interaction is predation, evinced by a type of small, circular boring found in one valve of *Amphistrophia funiculata* and two of *Nuculites antiqua*. Indirect evidence, considered below, suggests that predation may have played a larger role in the structure of Ludlow communities.

In modern marine communities, predators are known to have an important function in damping temporal fluctuations in densities and equalizing competition for space among prey species (Blegvad 1928; Paine 1966). Jackson (1972) found a correlation between low-diversity bivalve communities with low predation rates, and high-diversity, offshore bivalve communities experiencing higher rates of predation from a greater number of predatory taxa. Jackson suggested that high rates of predation generally contribute to higher diversities in level-bottom communities.

Apart from rare asteroids, potential predators among the Ludlow fauna of the Welsh Borderland include cephalopods, gastropods and phyllocarid crustaceans. The diversity of these groups increases toward the lower parts of the Ludlow column, in the distal shelf facies with higher diversity bottom communities (see Jones & Woodward 1888–89 and Blake 1882, as well as data in Appendix 3). Ludlow communities may therefore show a correlation between predator diversity and diversity of prey species, like that discussed by Jackson (1972). Highest and most constant rates of predation in Ludlow distal shelf environments might also have contributed to the relatively predictable, low-amplitude fluctuations of brachiopod species. These suggestions, though tantalizing, must remain tentative on the basis of present data.

Encrustation

The chief form of biotic interaction recorded in Ludlow faunas is encrustation, primarily of brachiopods, gastropods and cephalopods by a number of bryozoans, serpulids, cornulites, auloporids and boring organisms of unknown affinity. Some of these organisms can be seen on examples of *Isorthis orbicularis* (Pl. 5, fig. 1) and *Protochonetes ludloviensis* (Pl. 5, fig. 2). Preliminary observations of encrustation show little selectivity of host shells by encrusting organisms. They are overwhelmingly found on the external surfaces of shells, suggesting that many settled when the host was alive. Within samples, 1% or fewer of brachiopod and mollusc shells are encrusted and the lowest frequencies of encrustation occur in the *G. obovata* Association.

Under favourable conditions, the use of organisms by other organisms as hard substrates can produce enough interaction to result in an ordered ecological succession. Shäfer (1970) has described such a case in modern seas, and Walker & Alberstadt (1975) described a succession involving encrusting relations in the Ordovician. Encrustation within Ludlow shelf communities never reached the intensity of interaction in which an ecological succession could proceed. This was probably because of continual sedimentation, ensuring that the hard substrates provided by brachiopod and mollusc shells were always isolated and only temporarily available for colonization.

Were Silurian communities depth-related ?

Depth relations in modern benthic communities

Before summarizing the conclusions and general implications of the analysis of Ludlow shelf faunas, it is appropriate to consider the question of the depth relation of Silurian communities, which has coloured palaeoecological study of this period since the work of Ziegler (1965). In exhaustive studies of the environmental relations of modern benthic communities, Dörjes (1972) and Parker (1975) have shown that water depth is only one of a large number of factors which correlate with community distributions. Dörjes (1972) identified bottom morphology, grain size, sedimentation processes, relation to wave base and food supply as important influences on shelf communities off Georgia. Parker (1975) demonstrated statistical correlations between community distributions and current strength, grain size, turbulence, chemical state of the bottom and light penetration in Hadley Harbor, Massachusetts.

These studies show that many of the environmental factors relating to modern benthic communities revolve around the dynamic state of the sediment bottom. Where such conditions parallel bathymetry, and sedimentary facies zones are orientated parallel to the coastline, modern communities tend to occur in similar depth-related bands (Dörjes 1971, 1972). Where zones of similar sedimentary facies and hydrographic conditions are not parallel to the coastline or bathymetric contours, benthic communities show a similar lack of depth relation (Dörjes *et al.* 1969, 1970). These observations provide an important model for depth evaluation of ancient communities. They show that consistent depth relations of benthic communities are not intrinsic, but may be either present or absent, depending on the distribution of a complex of hydrographic factors.

Upper Llandovery communities of the Welsh Borderland

Ziegler (1965) and Ziegler *et al.* (1968*a*, 1968*b*) presented a picture of five communities occurring in consistent depth-related bands in the Upper Llandovery of Wales and the Welsh Borderland. Recent work on the sedimentology of these deposits by Bridges (1975) indicates that the depth relations of these communities is not as consistent as has been supposed. For C_1 times, Ziegler *et al.* (1968*b* : fig. 13) showed the control for their parallel bands of communities in a small area between Wenlock Edge and the Breidden Hills. Bridges (1975 : fig. 11A) has shown that this area did not possess an even bathymetric gradient, but included a southward-facing peninsula on the site of the Long Mynd. A *Lingula* Community lived east of this peninsula in the shallow sands of a restricted marine embayment. *Pentamerus* and *Stricklandia* Communities on the southern and western sides of the peninsula lived on open marine sands. Bridges' data suggest that position landward or seaward of the Long Mynd peninsula was the most important factor relating to community distribution.

By C_5 to C_6 times, the Welsh Borderland shelf possessed a fairly even bathymetric gradient with coarse to fine-grained sediments occurring in parallel bands away from the shoreline (Bridges 1975). The shelf communities at this time were also arranged in subparallel bands (Bridges 1975 : fig. 11B), and the community distributions shown by Ziegler *et al.* (1968*b* : fig. 14) were probably closely related to bathymetry. This situation follows from the modern observations, which show that depth-related conditions of sedimentation will result in depth-related community distributions.

General depth relations in Silurian communities

Like modern marine communities, those of the British Upper Llandovery appear to show variable relation to water depth, according to the orientation of sedimentation conditions. They do not provide evidence for any intrinsic depth zonation of Silurian bottom faunas, and their use as 'bathymetric standards' for the Silurian (Boucot 1975) is fallacious.

The relation between bathymetry and sedimentation conditions in determining Silurian community distributions can be shown by a comparison between a terrigenous shelf and a carbonate platform brachiopod association. The *Mesopholidostrophia laevigata* Association of the Welsh Borderland occupied terrigenous bottoms probably under several tens of metres of water. This depth range is indicated by the position of the community in the distal shelf end of Ludlow stratigraphic gradients, resemblance of its enclosing sediment to modern, offshore shelf deposits and the total absence of any nearby shoreline (Holland & Lawson 1963). Hurst (1975*b* : table 3) has described brachiopod assemblages of nearly identical generic content to the *M. laevigata* Association from the Ludlow-age Eke Beds of Gotland. The Eke Beds were deposited on a carbonate platform, and consist of argillaceous limestone with abundant calcareous algae. They underlie and possibly grade laterally into the Burgsvik Sandstone, a probably intertidal deposit. The Eke Beds can thus be considered as very shallow in nature, deposited beneath waters of possibly only a few metres in depth.

This example shows that similar generic associations of Silurian brachiopods lived at shallower depths on carbonate platforms than on terrigenous shelves. In the Welsh Borderland, the *M. laevigata* Association occupied an environment of relatively quiet water and low sedimentation rate. These conditions were met with in an offshore, relatively deep situation in the terrigenous shelf setting. On the carbonate platform of Gotland, however, such conditions of sedimentation appear to have occurred in much shallower water, because of the reduced influence of terrigenous sediment influx. Thus, the Gotland counterpart of the *M. laevigata* Association could inhabit shallower absolute depths.

Both the example given above and the review of British Upper Llandovery communities given here are completely in keeping with modern observations on communities and water depths. All community distributions relative to water depth, whether parallel or oblique to bathymetric contours, are essentially 'special cases' related to the local sedimentation and hydrographic conditions. Silurian communities may or may not be related to water depth, depending on these factors, and faunal data alone cannot be used to make bathymetric correlations between different times and places.

Summary and implications of Ludlow community organization

The environmental gradient and composition of fauna

Ludlow sections in the Welsh Borderland record a slow, terrigenous progradation over a marine shelf, interrupted locally by carbonate deposition. A general trend of shallowing, increase in grain size and sedimentation rate, increase in shell transport and increase in frequency and intensity of storm-sedimentation events is apparent from the base to the top of the Ludlow column. Except for carbonate interruptions, the Ludlow sections represent a vertically superposed gradient from distal shelf to proximal shelf environments. A shoreface environment is not preserved.

Articulate brachiopods are dominant in number of individuals, but not of species, through the broad range of shelf environments, decreasing in diversity from the distal to proximal shelf. Only in relatively high-stress shelf environments is the abundance of articulate brachiopods approached or surpassed by that of other groups. These environments include deoxygenated distal shelf muds, rapidly-deposited proximal shelf silts and the brackish-water facies of the Downtonian.

Bivalves are locally abundant in distal shelf muds and proximal shelf silts, but generally comprise a small proportion of individuals within communities. They decrease in diversity along the distal to proximal shelf gradient, with distal shelf communities characterized by very sporadic occurrence of a large number of bivalve species. Gastropods also decrease in diversity from distal to proximal shelf communities. They are consistently present, but seldom abundant. Cephalopods are represented by pelagic and nektobenthic forms. Pelagic forms are abundant in distal shelf sediments, while nektobenthic forms are found in consistent low abundance through the whole shelf transect, and were probably predators.

Corals, bryozoa and crinoids show a preferential occurrence in distal shelf silts, where sedimentation was slow, but periodic agitation occurred. They decrease in abundance into proximal shelf silts with relatively high sedimentation rates, and also become rare in distal shelf muds. Trilobites are most abundant and diverse in distal shelf muds, but extend in low abundance across the full range of shelf environments. Minor groups of arthropods, annelids, echinoderms and small conoidal shells occur sporadically through various communities.

Trophic structures in Ludlow shelf communities indicate a mixture of deposit feeding and suspension feeding, with both abundant infauna and epifauna. Except where bryozoa and crinoids were common, little stratification occurred among the epifauna, and most suspension feeding probably occurred 0–2 cm above the substrate.

Dominance of physical factors in Ludlow community organization

The physical environment appears to have been paramount over biotic factors in shaping community patterns within Ludlow sections. The basic number and level of discreteness of Ludlow communities is a product of the history of environmental change. Long-term persistence of major sedimentary and hydrographic conditions produced extended stratigraphic intervals with relatively constant faunal content. Shorter intervals of environmental change produced subordinate stratigraphic intervals of faunal alteration and gradations between communities. An alternation of these phenomena produced the major stratigraphic pattern of Ludlow communities in the Welsh Borderland.

Stratigraphic variation occurs within communities in parts of sections representing stability in major environmental conditions. This variation does not lead to any progressive biological accommodation or increase in species diversity, and does not correspond to models of ecological succession. It consists of extreme and unpredictable fluctuations in the abundance of individuals of species in proximal shelf communities. In distal shelf environments, the intracommunity variation occurs mainly as lower amplitude, predictable cycles in abundance of species. These cycles are independent of faunal destructions represented by bentonites and storm-deposited silts. The cycles of one species do not consistently relate to those of others, or to any consistent patterns in diversity variation. The total pattern of temporal variation within communities does not conform to the repetition involved in ecological succession. Environmental influences upon the survival of pelagic larvae, and not events or interactions in the bottom environment, are the best model for intracommunity variation in Ludlow sections.

Except for minor sediment conditioning, ecological succession was probably precluded in Ludlow shelf environments by a lack of biotic control over the physical environment. Continued sediment dilution of benthic populations would have prevented the concentrated use of other organisms as substrates, and confronted newly-recruited larvae, on the average, with the same type of sediment bottom occupied by their parents. Sediment dilution of organic remains would preclude the inheritance of accumulated biological information, as discussed by Margalef (1968), which is necessary for new generations to proceed beyond the organizational state of their predecessors. In this situation, only a change in the external environment can cause an alteration of community structure.

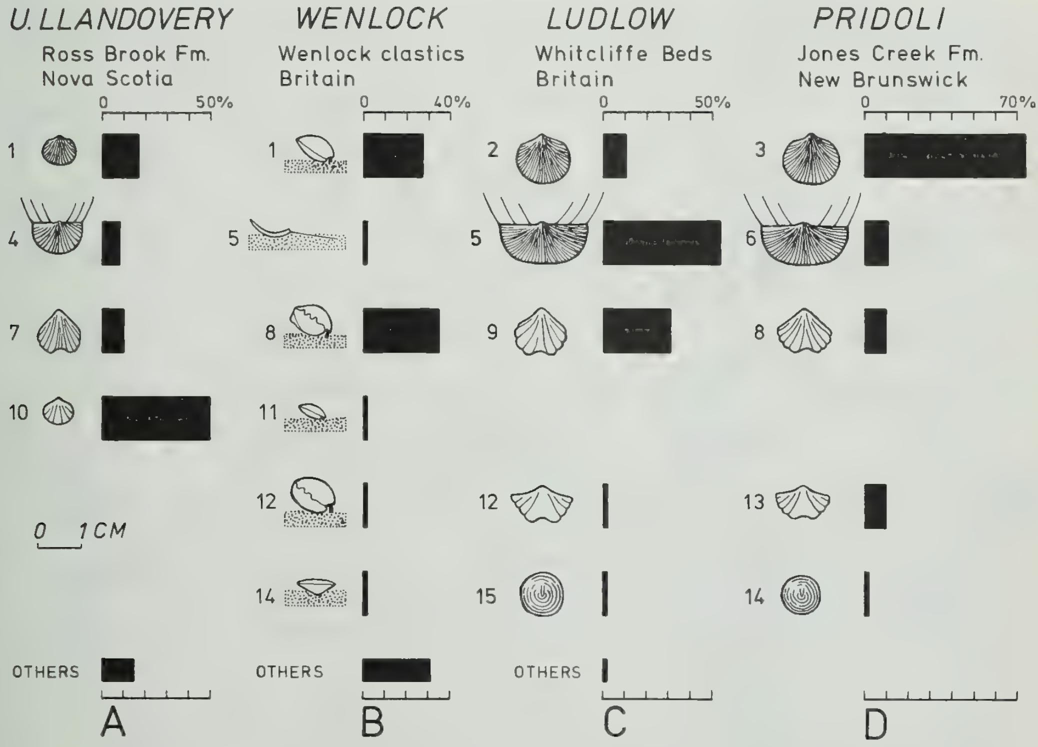

Fig. 26 Local examples of the *Salopina* Parallel Communities. Column B shows inferred life positions, and columns A, C and D show ventral views of the pedicle valve; low abundances are exaggerated to 2%. A – 'mixed *Salopina conservatrix* – *Eocoelia* Communities' of Watkins & Boucot (1975); B – *Salopina* Community of Calef & Hancock (1974); C – *Protochonetes ludloviensis* Association of this report; D – *Salopina submedia* Community of Watkins & Boucot (1975). 1 – *Salopina conservatrix* (McLearn); 2 – *S. lunata* (Sowerby); 3 – *S. submedia* (McLearn); 4 – *Protochonetes tenuistriata* (Hall); 5 – *P. ludloviensis* Muir-Wood; 6 – *Protochonetes* sp.; 7 – '*Camarotoechia*' *rossonia* McLearn; 8 – '*Camarotoechia*' spp.; 9 – '*C.*' *nucula* (Sowerby); 10 – *Eocoelia sulcata* (Prouty); 11 – *E. angelini* (Lindström); 12 – *Howellella elegans* (Muir-Wood); 13 – *Howellella* sp.; 14 – *Orbiculoidea* sp.; 15 – *O. rugata* (Sowerby).

The Ludlow fauna corresponds to the stability-time hypothesis in showing highest species diversity in the low-stress distal shelf environment. Rollins & Donahue (1975) have used such diversity relations to infer the existence of biological accommodation in such communities, a type of biotic interaction which can lead to progressive niche-partitioning and diversity increase. As Ludlow communities of distal shelf environments show no increase in diversity with temporal persistance of low-stress conditions, and do not show a successional pattern in cycles of species, they were probably not biologically-accommodated. If predation was important in the high-diversity communities, as suggested in the biotic interaction section, p. 249, it contributed to an overall stability in diversity and not a general increase.

An alternative explanation for high diversity in distal shelf environments is a simple correspondence of their physical conditions to the physiologic optima of the largest set of Ludlow shelf species. This relation has been expressed by Gibson & Buzas (1973) as the 'carrying capacity' of a particular environment, which remains constant through time.

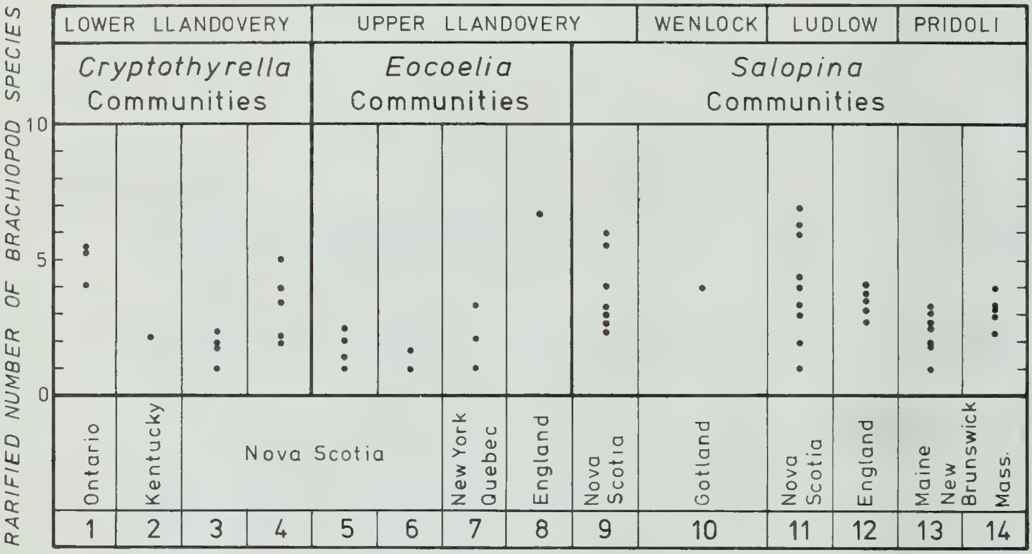

Fig. 27 Species diversity in parallel communities of the proximal shelf region. Each point represents a single sample, rarified to a diversity value at 50 individuals. In the list of data sources for this and following figures, 'USNM' indicates the number of a United States National Museum collection for which brachiopod data have been provided to the author by A. J. Boucot. These unpublished data are available on request. 1 – Manitoulin Dolomite, USNM 11582, 11584, 11585; 2 – Brassfield Limestone, USNM 11643; 3 – Beechhill Cove Formation, the *Cryptothyrella* Community of Watkins & Boucot (1975); 4 – Beechhill Cove Formation, the *Mendacella* Community of Watkins & Boucot (1975); 5 – Middle Member of Ross Brook Formation, the *Eocoelia* Community of Watkins & Boucot (1975); 6 – Upper Member of Ross Brook Formation, the *Eocoelia* Community of Watkins & Boucot (1975); 7 – Clemville Formation USNM 11107, Sodus Shale USNM 12018, Hickory Corners Limestone USNM 11897; 8 – Damery Beds, USNM 10217; 9 – Upper Member of Ross Brook Formation, the mixed *Salopina conservatrix* – *Eocoelia* Communities of Watkins & Boucot (1975); 10 – Klinteberg Beds, Hurst (1975*b*); 11 – Moydart Formation, the *Salopina submedia* – '*Camarotoechia*' aff. *planorugosa* Community of Watkins & Boucot (1975); 12 – Whitcliffe Beds, the *Protochonetes ludloviensis* Association of this report; 13 – Pembroke Formation, the *Salopina submedia* and *Protochonetes* Communities of Watkins & Boucot (1975); 14 – Jones Creek Formation, Newbury Volcanic Group, Ames Knob Formation and Pembroke Formation, the *Salopina submedia* Community of Watkins & Boucot (1975).

This discussion leads to the conclusion that both high diversity and low diversity communities in Ludlow sections were essentially under the external control of the physical environment. Physical environmental changes were necessary to effect any major change in faunal composition, population patterns or diversity of the shelf fauna. In Ludlow sections, changes in bottom type, sedimentation patterns and hydrographic conditions were the physical factors which exerted most influence upon fauna. In the absence of such changes, the same set of species continued colonizing the accumulating sediment bottoms, with pelagically-influenced variation in larval recruitment.

Consequence of physical control of Silurian shelf communities

The simple physically-controlled organization inferred for Ludlow shelf faunas has general implications for the Silurian record. There appears to be no intrinsic biotically-controlled change within Ludlow shelf communities. The consequence of this type of organization is expressed throughout Silurian time as relatively steady-state levels of diversity within level-bottom communities.

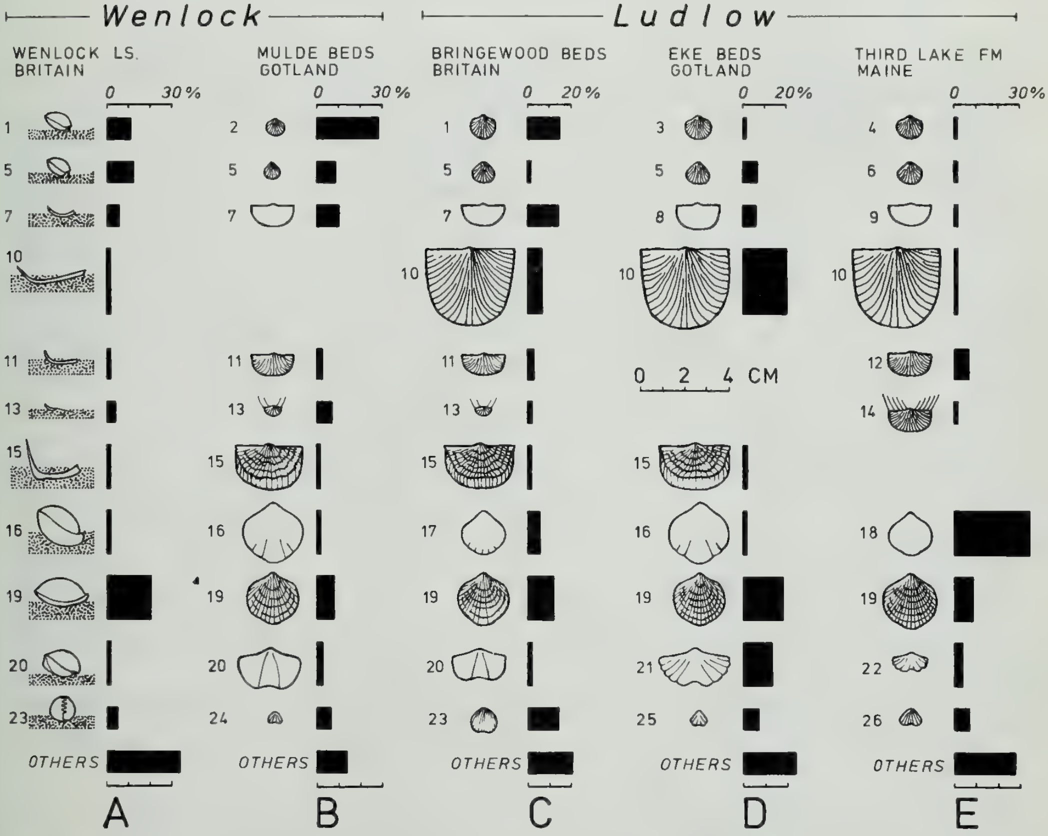

Fig. 28 Local examples of the Stropheodontid Parallel Communities, using data from A, Hurst (1975*c*); B, D, Hurst (1975*b*); C, this report; and E, USNM 11357, 11364, 11630. 1 – *Isorthis clivosa* Walmsley; 2 – *I. crassa* (Lindström); 3 – *I. canaliculata* (Lindström); 4 – *I.* cf. *arcuaria* (Hall & Clarke); 5 – *Dalejina hybrida* (Sowerby); 6 – *Dalejina* sp.; 7 – *Mesopholidostrophia laevigata* (Sowerby); 8 – *Brachyprion* sp.; 9 – *Mesopholidostrophia* sp.; 10 – *Strophonella euglypha* (Hisinger); 11 – *Amphistrophia funiculata* (M'Coy); 12 – *A.* cf. *funiculata* (M'Coy); 13 – *Protochonetes minimus* (Sowerby); 14 – '*Chonetes*' *jerseyensis* Hall; 15 – *Leptaena depressa* (Sowerby); 16 – *Gypidula galeata* (Dalman); 17 – *Gypidula lata* Alexander; 18 – *Gypidula* sp.; 19 – *Atrypa reticularis* (Linnaeus); 20 – *Eospirifer radiatus* (Sowerby); 21 – *Striispirifer striolatus* (Lindström); 22 – *Delthyris* sp.; 23 – *Sphaerirhynchia wilsoni* (Sowerby); 24 – *Ancillotoechia bidentata* (Hisinger); 25 – '*Camarotoechia*' *nucula* (Sowerby); 26 – *Ferganella* sp.

Parallel communities (Thorson 1957) are characterized by recurrent associations of genera on a nearly world-wide scale, and are well developed among Silurian brachiopods (Boucot 1975). Within Silurian proximal shelf faunas, a replacement from Lower Llandovery through to Pridoli times occurs from the *Cryptothyrella* Communities through *Eocoelia* Communities to *Salopina* Communities (Watkins & Boucot 1975). Some local examples of the *Salopina* Communities, including the *P. ludloviensis* Association of the Welsh Borderland, are shown in Fig. 26, and provide an illustration of the parallel community phenomenon. Like the *P. ludloviensis* Association, other local examples of these communities show a low diversity of brachiopods. This diversity pattern is shown in Fig. 27, and remains quantitatively stable throughout the Silurian.

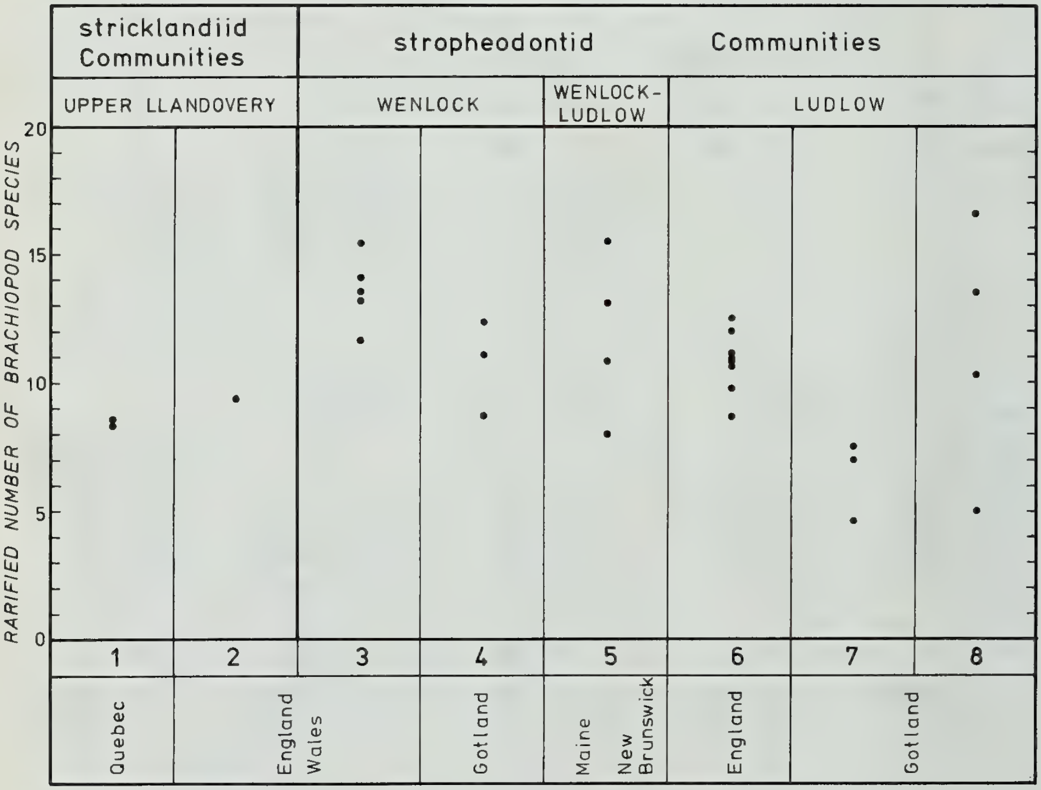

Fig. 29 Species diversity in the Stricklandiid and Stropheodontid Parallel Communities. Each point represents a single sample, from: 1 – La Vieille Formation USNM 11450, Val Brillant Quartzite USNM 11133; 2 – Wych Beds, the *Costistricklandia* Community of Ziegler *et al.* (1968*b*); 3 – Wenlock Limestone, the *Isorthis clivosa* Community of Hurst (1975*c*); 4 – Mulde Beds, Hurst (1975*b*); 5 – Third Lake Formation USNM 11357, 11364, 11630, Mascarene Series USNM 11917; 6 – Lower Bringewood Beds, the *Mesopholidostrophia laevigata* Association of this report; 7 – Hemse Beds, Hurst (1975*b*); 8 – Eke Beds, Hurst (1975*b*).

More diverse distal shelf or carbonate platform communities, like the *M. laevigata* Association, also exist as parallels throughout the Silurian. In the Llandovery, local examples are often dominated by stricklandiids (Ziegler *et al.* 1968*a*), and in the post-Llandovery, stropheodontid brachiopods are one of the characteristic forms. The Stropheodontid Parallel Communities show striking similarities between different areas and times, and are illustrated in Fig. 28. Diversity of these communities is plotted in Fig. 29, and also shows a general stable level throughout Silurian time.

The *Dicoelosia* Communities are another group of parallel associations among Silurian brachiopods. This suite of dominantly distal shelf, muddy bottom communities has been named the *Dicoelosia–Skenidioides* Community Group by Boucot (1975), and is represented by the *G. obovata* Association in the Ludlow of the Welsh Borderland. Although brachiopod diversity in these communities is highly variable, a plot through Silurian time shows a general stability in number of species present (Fig. 30).

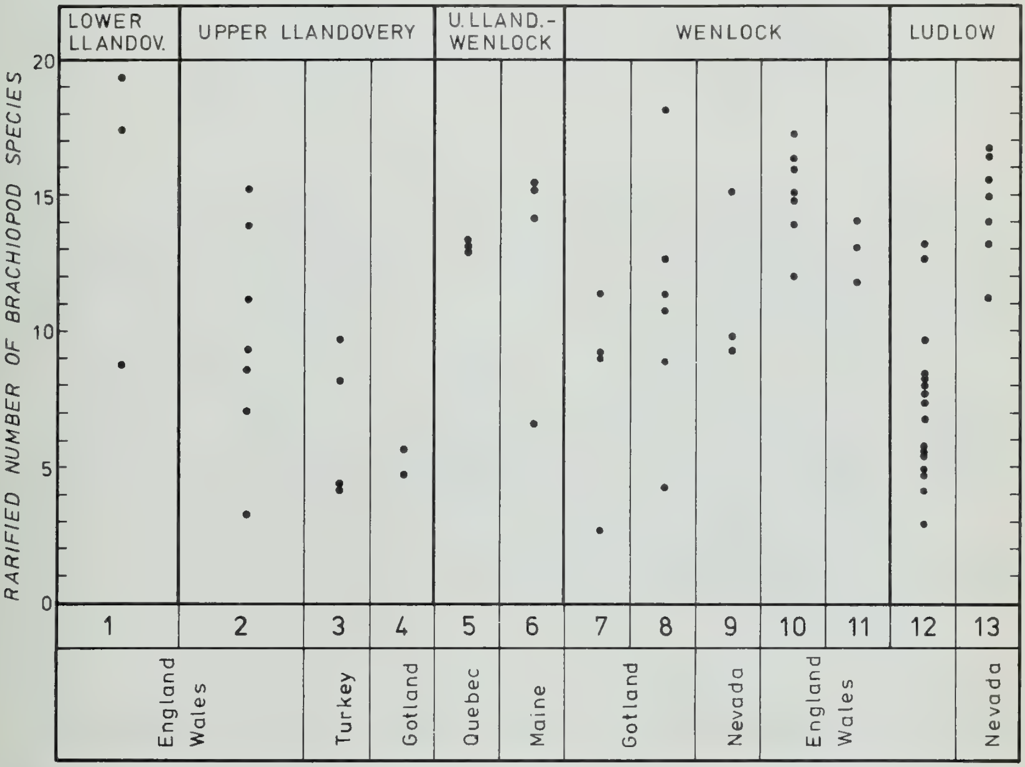

Fig. 30 Species diversity of the *Dicoelosia* Parallel Communities. Each point represents a single sample, from: 1 – Gasworks Mudstone USNM 10509, siltstone near Meifod, Temple (1970), limestone bands at Keisley, Temple (1968); 2 – C_1 to C_6 age beds, USNM 10259, 10260, 10514, 10512, 10272, 10257, 10258; 3 – Umur-Dere-Folge (A III 3), USNM 10678, 10679, 10681, 10686; 4 – Lower Visby Beds, Hurst (1975*b*); 5 – Pointes-aux-Trembles Formation, USNM 11173, 11490, slates at Lac des Eaux Mortes USNM 11194; 6 – Perham Formation 11174, 13029, Dennys Formation USNM 11850, 11870; 7 – Upper Visby Beds, Hurst (1975*b*); 8 – Högklint Beds, Hurst (1975*b*); 9 – Hidden Valley Dolomite, USNM 12879, 13617, 17417; 10 – Woolhope Limestone, *Eoplectodonta duvalii* Community of Hurst (1975*c*); 11 – Wenlock Limestone, *E. duvalii* Community of Hurst (1975*c*); 12 – Middle Elton Beds, *Glassia obovata* Association of this report; 13 – Roberts Mountains Formation, Johnson *et al.* (1976).

The steady-state diversities within Silurian shelf communities of brachiopods through tens of millions of years has been previously discussed by Boucot (1975). It provides direct evidence that biological accommodation leading to progressive diversity increase did not occur in either low diversity or high diversity communities through Silurian time. The phyletic evolution in Silurian brachiopods must therefore have primarily involved niche replacements within stable community structures, rather than niche diversification or partitioning. The analysis of Ludlow shelf faunas in the Welsh Borderland suggests that this long-term stability of community structure resulted from a primary control of faunal patterns by the external physical environment.

Acknowledgements

I am grateful to J. M. Hurst for invaluable encouragement through this project, and joint participation in the study of *Isorthis*. I also wish to thank C. J. Aithie, W. B. N. Berry, A. J. Boucot, A. Hallam, A. P. Heward, R. A. Hewitt, J. G. Johnson, M. Lockley, W. S. McKerrow, R. M. Sykes and A. Williams for help in many ways. £200 toward the work was provided by the Burdett-Coutts Foundation of the University of Oxford, and facilities for preparing the manuscript were made available by the University of California Museum of Paleontology, Berkeley.

Appendix 1. Location of measured sections

Area 1. Millichope

Section 1B. This section is 4·1 m thick, in an old quarry on a hillside due N of Holloway Farm, SO 53608944. It is entirely within the Upper Leintwardine Beds (Shergold & Shirley 1968), and sample numbers 1B1–1B6 were assigned.

Section 1C. This section is 8·1 m thick, in very low, overgrown exposures on W side of a lane bordering Millichope Park, 126 m south of junction of this lane with Holloway to Upper Millichope road, SO 52888900. Samples 1C1–1C2 were collected from the Upper Leintwardine Beds, and samples 1C3–1C8 from the Lower Leintwardine Beds.

Section 1D. 3·9 m of strata measured in a small quarry on N side of Holloway to Upper Millichope road, directly opposite house at entrance to Millichope Park, SO 52748911. Assigned to the Lower Bringewood Beds (Shergold & Shirley 1968). Samples 1D1–1D10 were collected.

Section 1E. 15·8 m of strata measured in stream section on NE side of Holloway to Upper Millichope road near Upper Millichope, between SO 52048959 (base of section) and SO 52128943 (top of section). The section is within the Middle Elton Beds, and samples 1E1–1E16 were collected.

Area 2. Ludlow

Section 2A. 0·6 m of strata measured on N bank of 'Ludford Lane', 106 m W of its junction with the A49, SO 51157413. Sample 2A1 is from the Ludlow Bone Bed, and 2A2 and 2A3 from the underlying Upper Whitcliffe Beds.

Section 2B. 10·4 m of strata measured at loc. 6 of Holland *et al.* (1963), the type section for the Upper Whitcliffe–Lower Whitcliffe boundary, SO 50967414. Samples 2B1–2B7 were collected from the Upper Whitcliffe Beds, and 2B8–2B9 from the Lower Whitcliffe Beds.

Section 2C. 23·8 m of strata measured at locs 3 and 8 of Holland *et al.* (1963), including the type boundaries for the bases of the Lower Whitcliffe Beds and Upper Leintwardine Beds, SO 50717428 (base of section) to SO 50717425 (top of section). Samples 2C1–2C9 were collected from the Lower Whitcliffe Beds, 2C10–2C15 from the Upper Leintwardine Beds and 2C16–2C19 from the Lower Leintwardine Beds.

Section 2D. 17·8 m of strata measured at loc. 30 of Holland *et al.* (1963), the type section for the Lower Leintwardine–Upper Bringewood boundary, SO 49537255. Samples 2D1–2D11 were collected from the Lower Leintwardine Beds, 2D12–2D15 from the Upper Bringewood Beds.

Section 2E. 3·4 m of strata measured in a small cutting on S side of the Whitcliffe Spur Road, and in low dip exposures immediately adjacent. Section at W border of landslip, SO 47227376. It is within the Upper Bringewood Beds, and samples 2E1–2E3 were collected.

Section 2F. 5·1 m of strata measure on N side of forestry track in Mary Knoll Valley, at type section for Lower Bringewood–Upper Elton boundary (Holland *et al.* 1963 : fig. 12), SO 48737292. Samples 2F1–2F3 were collected from the Lower Bringewood Beds, and 2F4–2F5 from the Upper Elton Beds. This section is very poorly exposed, and the boundary of these units was covered at the time of observations.

Section 2G. 0·9 m of strata measured in small exposure on S side of Old House Road at loc. 30 of Lawson (1973*b*), SO 48327257. This exposure is in the Upper Elton Beds, and was assigned sample number 2G1.

Section 2H. 2·6 m of strata measured in small cutting on N side of Hazel Coppice Road, at W end of loc. 27 of Lawson (1973*b*), SO 47597350. The section is in the Upper Elton Beds, and sample numbers 2H1–2H4 were assigned.

Section 2I. 3·6 m of strata measured in cutting at junction of forestry roads on W side of High Vinnals, loc. 70 of Lawson (1973*b*), SO 47507161. The section is in the Middle Elton Beds, and samples 2I1–2I6 were collected.

Section 2J. 7·2 m of strata measured in deep double-sided cutting on S side of Goggin Road at loc. 69 of Lawson (1973*b*), SO 47437171. The section is near the base of the Middle Elton Beds, and samples 2J1–2J12 were collected.

Area 3. Woodbury Quarry

Section 3A. A single section, 163 m thick, measured in Woodbury Quarry, from SO 74256363 (top of section) to SO 744637 (base). Samples 3A1–3A26 were collected from the Whitcliffe Beds, 3A27–3A29 from the Upper Leintwardine Beds, 3A30–3A48 from the Lower Leintwardine Beds, 3A49–3A51 from the Upper Bringewood Beds and 3A52–3A120 from the Lower Bringewood Beds. All units but the Whitcliffe Beds were being actively quarried, and the amount of Lower Bringewood Beds exposed from time to time varied. Small faults, of undetermined displacement, occur at 65·87 m and 71·45 m above base of section.

Area 4. Ledbury

Section 4A. 52·5 m of strata measured at N end of Frith Wood, in section described by Penn *et al.* (1971 : fig. 9). The base of this section, SO 72304024, is located at SW corner of junction of forestry tracks named Top Walk and Godwin's Rise. From this point, the section was measured downhill (SW) along S bank of Godwin's Rise, for 280 m along this track; top of section SO 72064011. Samples 4A1–4A26 were collected from the Whitcliffe Beds, 4A27–4A29 from the Upper Leintwardine Beds, 4A30–4A54 from the Lower Leintwardine Beds and 4A55–4A58 from the Upper Bringewood Beds.

Section 4B. 77·6 m of strata measured in old quarry on N side of Knapp Lane, from SO 71403857 (base of section) to SO 71313858 (top), immediately outside Ledbury. Samples 4B1–4B26 were collected from the Lower Bringewood Beds and 4B27–4B35 from the Upper Elton Beds. Several small faults, of undetermined displacement, occur between 36 m and 55 m above base of section.

Section 4C. 5·8 m of strata measured at loc. 22 of Penn *et al.* (1971 : fig. 8), in NE bank at junction of two lanes, SO 71523857. This section is in the Middle Elton Beds, and samples 4C1–4C4 were collected.

Area 5. Perton

Section 5A. 6·1 m of strata measured in southernmost of series of old quarry faces S of Perton, on E side of Perton Lane, SO 59694031. This section is shown at loc. 2 by Curtis *et al.* (1967 : fig. 5). It is in the Upper Whitcliffe Beds, and samples 5A1–5A6 were collected.

Section 5B. 2·9 m of strata measured in small cutting on E side of Perton Lane, immediately S of where a footpath meets the lane, SO 59674033. This section is shown as loc. 3 by Curtis *et al.* (1967 : fig. 5). It is in the Lower Whitcliffe Beds, and samples 5B1–5B3 were collected.

Section 5C. 13·5 m of strata measured in overgrown exposures in E bank of Perton Lane, from SO 59694024 (top of section) to SO 59614013 (base). Samples 5C1–5C5 were collected from the Lower Whitcliffe Beds, 5C6–5C8 from the Upper Leintwardine Beds and 5C9–5C13 from the Lower Leintwardine Beds. The Upper Leintwardine Beds in this section are shown as loc. 4 by Curtis *et al.* (1967 : fig. 5), at SO 59634018.

Section 5D. 18·4 m of strata measured in Perton Quarry, on the main W face (Pl. 3, fig. 2) and an upper SW face immediately adjacent, SO 59523995. Samples 5D1–5D10 were collected from the Lower Leintwardine Beds, and 5D11–5D12 from the Upper Bringewood Beds.

Section 5E. 15·4 m of section measured S of Perton Quarry, in discontinuous exposures in E bank of Perton Lane from SO 59583992 (top of section) to SO 59613977 (base). This section is in the Lower Bringewood Beds, and samples 5E1–5E10 were collected.

Section 5F. 2·7 m of strata measured in small exposures in both E and W banks of Perton Lane immediately NW of farmhouse at Copgrove, SO 59643964. This section is in the Lower Bringewood Beds, and samples 5F1–5F3 were collected.

Section 5G. 7·4 m of strata measured in small cutting and other limited exposures in W bank of lane between Tower Hill and Wootton, at a bend in lane at SO 59253950. This section is shown as loc. 7 by Curtis *et al.* (1967 : fig. 5). Sample 5G1 was collected from the Lower Bringewood Beds and 5G2–5G7 from the Upper Elton Beds.

Section 5H. 7·6 m of strata measured in E bank of lane between Tower Hill and Wootton at SO 59223940. This section is in the Upper Elton Beds, and samples 5H1–5H7 were collected.

Section 5I. 38·6 m of strata measured in E bank of lane between Tower Hill and Wootton, between SO 59223935 (top of section) and SO 59233918 (base). These exposures are interrupted by the drive into Tower Hill Cottage (which is not actually on Tower Hill). The section is in the Middle Elton Beds, and samples 5I1–5I29 were collected.

Appendix 2. Reliability of faunal sampling

Definitions and procedures

As discussed earlier, density measurements are not adequate for standardization of palaeontological samples from a variety of sedimentary facies, and counts of numbers of individuals (as defined in methods section, pp. 178–9) have been used for this purpose. Samples processed for this project represent a variety of rock volumes and vary in content from 10 to 700 individuals. In the following discussions, 'sample size' refers exclusively to the number of individuals per sample. Representative sample sizes are given in Appendix 3, Tables 17–20. Most samples contained 50–75 individuals.

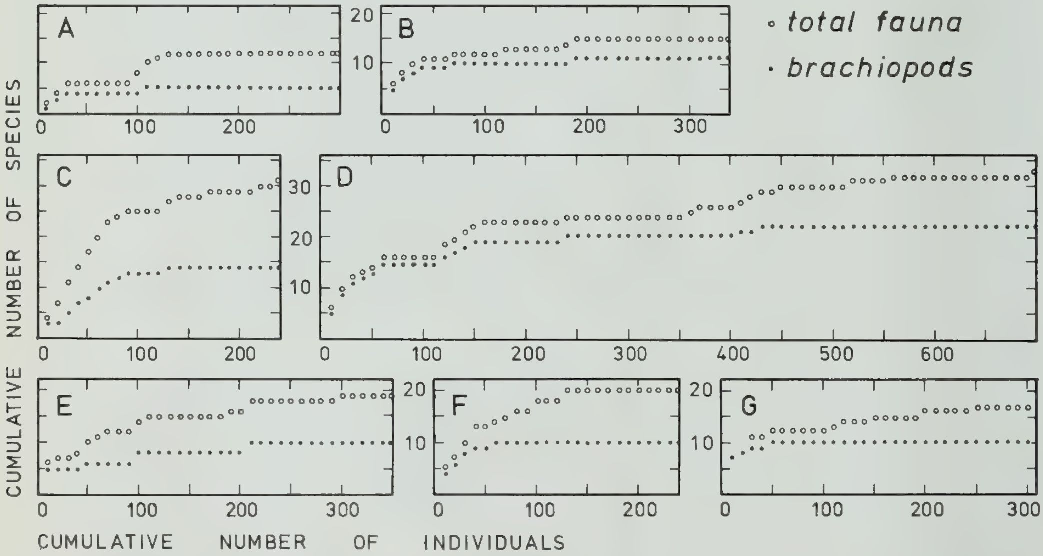

Fig. 31 Relation of number of individuals counted to number of species obtained in single samples. A – sample 4A7, *Protochonetes ludloviensis* Association; B – sample 4A44, upper phase of *Sphaerirhynchia wilsoni* Association; C – sample 4B31, 'transition fauna'; D – sample 4C1, *Glassia obovata* Association; E – sample from the Lower Leintwardine Beds at Chance's Pitch (SO 750402), upper phase of *S. wilsoni* Association; F – sample 4A29, *Shaleria ornatella* Association; G – sample 4A28, *S. ornatella* Association.

Relation of sample size to measured properties of samples was evaluated by the following method. In each of eight large samples from a variety of communities and sediments, all fossil specimens were listed in the order in which they appeared on fissile surfaces during processing of the rock. This order of appearance is considered random. From such lists, the content of each sample was calculated separately at 10-individual intervals for sample sizes ranging from 10 to over 240 individuals. The data were used to construct curves for each sample showing changes in measured properties with change in sample size. This procedure is the basis for the following discussions.

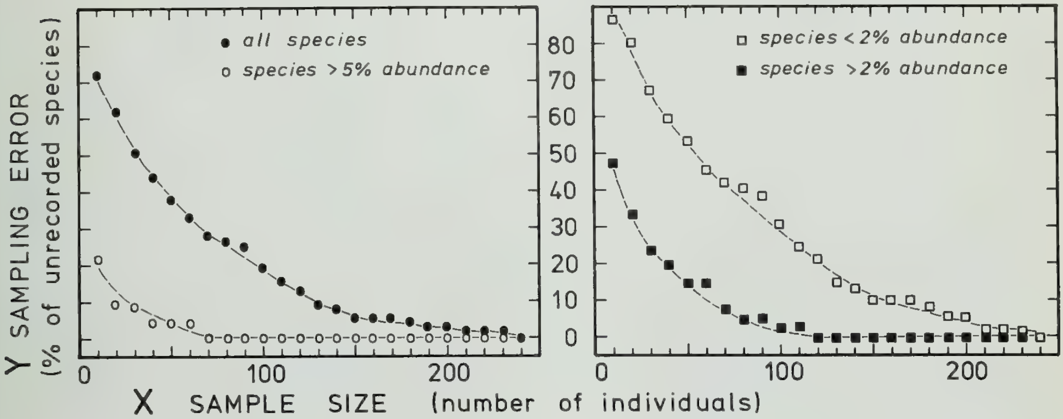

Fig. 32 Percentage of unrecorded species at different sample sizes, where 240 individuals are arbitrarily considered to yield 100% of species. These curves are based on data in Fig. 31. The sampling error, Y, was calculated as follows: samples A, B, C, E, F, & G of Fig. 31 yielded 104 total species at sample sizes of 240 individuals (62 species $<2\%$ relative abundance, 42 species $>2\%$, 23 species $>5\%$). At counts of 10, 20, 30 individuals, etc., the number of species recorded in these samples was divided by the number at 240 individuals. This value was then subtracted from 100% to obtain Y. See text for discussion of results.

Presence/absence criteria for species

Fig. 31 shows the increase in number of species obtained with increasing sample size. Beyond 200 individuals, most species curves remain constant or increase at a very slow rate. The number of species obtained at 240-individual sample size was arbitrarily assigned a value of 100% for comparison with species numbers in smaller samples. Results of this procedure are given in Fig. 32. Species with relative abundances above 5%, which include those used for the characterization of communities, were obtained at all sample sizes above 70 individuals. Rarer species, especially those comprising less than 2% of fauna in samples, had a much poorer rate of recovery (Fig. 32). Failure to record these species at sample sizes below 200 individuals is not conclusive evidence of their absence from any given area of rock.

Measurement of relative abundance

Relative abundances for each form within samples are defined, as a percentage, as the number of individuals of the form divided by the total number of individuals in a sample. Fig. 33 shows the relation between increasing sample size and measurements of relative abundance. Relative abundance values for each species show fluctuations within the same sample between sample sizes of 10 and 150 individuals, and stabilize above 200 individuals. Absolute stabilization is not seen in the curves, however, and measurement of relative abundance beyond the nearest 1% is not valid for even the largest samples used here.

The following method was used to compare the reliability of relative abundance measurements at different sample sizes. The error in measurement of the relative abundance of any species is arbitrarily set at 0 in a sample size of 200 individuals. The difference between the relative abundance for a species in a 200-individual sample and its relative abundance at any other sample size is d. Twenty-one species, all with relative abundances over 5%, were used in calculating d values at 24 sample sizes from 10 to 240 individuals.

The average error in relative abundance, specific for a particular sample size, is designated as Y, and calculated as:

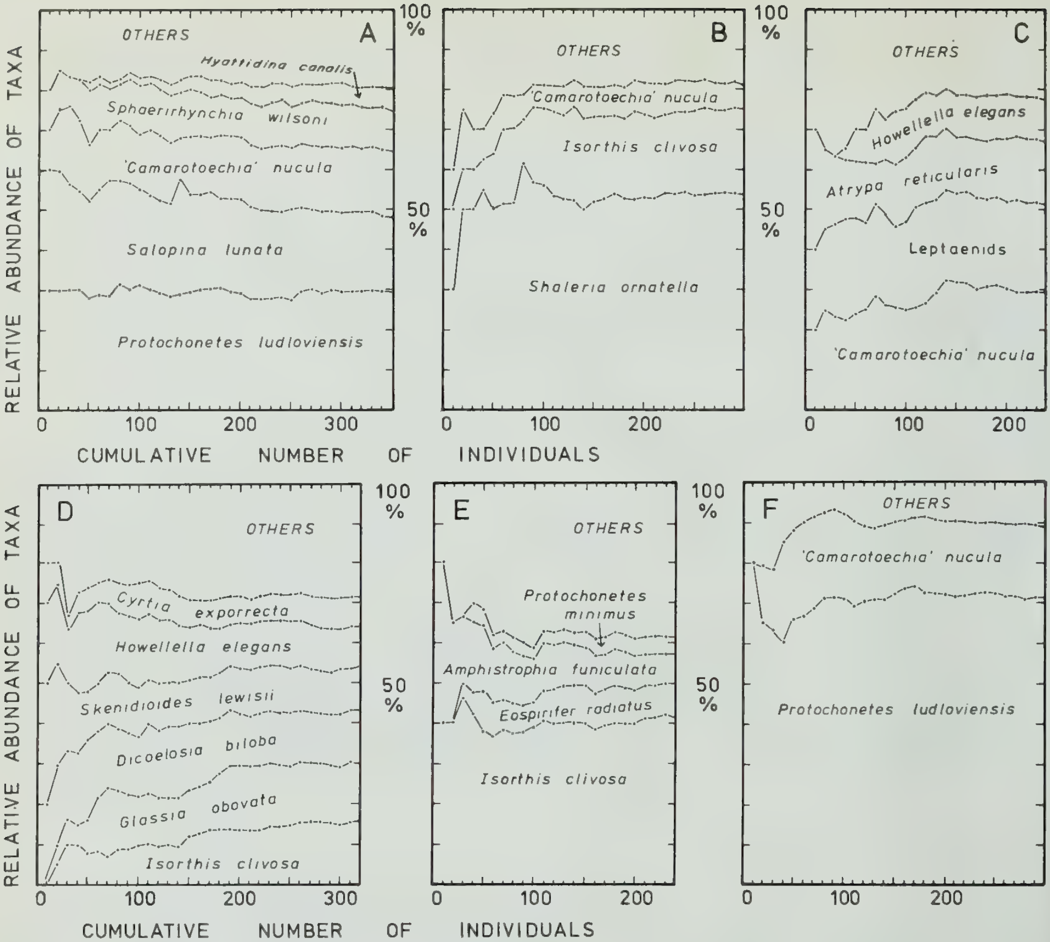

Fig. 33 Relation of increasing sample size to the measurement of relative abundances. A – sample from Chance's Pitch; B – sample 4A28; C – sample 4A29; D – sample 4C1; E – sample 4B31; F – sample 4A7.

$$\frac{\sum |d|}{21} = Y$$

Plots of Y values against sample size are shown in Fig. 34. As an absolute value, the average error in measurement of relative abundance per species is 3% or less at sample sizes above 50 individuals. These results indicate that once a species has been recorded in samples above this size, the measurement of its relative abundance is fairly accurate.

Appendix 3. Faunal lists

The following tables present a small part of the quantitative faunal data which form the basis for this study. The full data are deposited in the Library of the British Museum (Natural History), Cromwell Road, London. They comprise 54 typewritten sheets giving faunal counts for 417 samples in the measured sections. These data should be consulted by anyone wishing to make comparisons with the community analysis presented here. Tables 17–20 are extracts from the complete data, and show the format used.

Tables 15 and 16, which follow, record the total faunal content of each Association, based on total counts for all their assigned samples. These tables tell nothing of the variability within the associations,

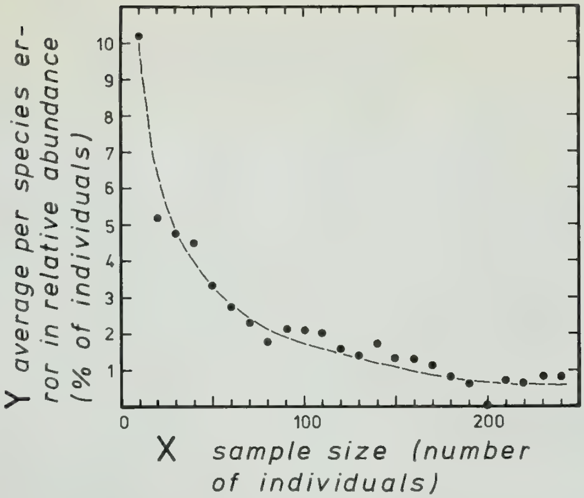

Fig. 34 Average error in measurements of relative abundance, based on calculations discussed in text. The curve was constructed for species whose relative abundances are above 5%. The error in measuring relative abundances for rarer species would fall below the curve.

and should not be taken as a 'fixed' definition of an association. Tables 17–20 give selected sample-by-sample data for some of the major associations, and provide examples of the basic data used in constructing the graphic faunal profiles.

Table 15 Cumulative faunal content for samples assigned to the following associations: Go1 – *G. obovata* (laminated shale facies); Go2 – *G. obovata* (mudstone facies); tr – transition fauna; Ml – *M. laevigata*; lpSw – lower phase of *S. wilsoni*; AC – *A. reticularis* – coral. Species marked with an asterisk are considered to be pelagic, and their numbers are not included in the final total of individuals

Association	Go1	Go2	tr	Ml	lpSw	AC
ANTHOZOA						
Favosites cf. *forbesi* (Edwards & Haime)	–	–	–	–	1	–
Rhabdocyclus porpitoides (Lang & Smith)	–	–	–	7	1	–
solitary trochoid corals	–	24	12	141	34	100
syringoporid	–	1	5	3	–	–
BRYOZOA	–	1	72	597	285	122
BRACHIOPODA						
Aegiria grayi (Davidson)*	×	14 000	20	–	–	–
ambocoelid	–	–	–	4	3	–
Amphistrophia funiculata (M'Coy)	–	1	36	225	11	–
Atrypa reticularis (Linnaeus)	–	3	66	867	312	347
'*Camarotoechia*' *nucula* (J. de C. Sowerby)	–	–	–	31	102	23
Coolinia pecten (Linnaeus)	–	–	–	1	4	2
Craniops implicata (J. de C. Sowerby)	–	239	15	130	52	–
Cyrtia exporrecta (Wahlenberg)	–	42	3	1	–	–
Dalejina hybrida (J. de C. Sowerby)	–	53	28	119	170	–
Dayia navicula (J. de C. Sowerby)	–	1	193	3	–	–
Delthyris sp.	–	–	–	1	–	–
Dicoelosia biloba (Linnaeus)	–	116	–	–	–	–
Eospirifer radiatus (J. de C. Sowerby)	–	5	60	70	3	1

Table 15 continued

Association	Go1	Go2	tr	M1	lpSw	AC
Gasconsia sp.	–	–	–	2	–	–
Glassia obovata (J. de C. Sowerby)	27	603	–	–	–	–
Gypidula lata Alexander	–	37	10	448	78	2
Howellella elegans (Muir-Wood)	1	206	162	355	1223	10
Hyattidina canalis (J. de C. Sowerby)	–	–	–	–	1	1
Isorthis clivosa Walmsley	–	1675	223	1041	–	–
Isorthis orbicularis (J. de C. Sowerby)	–	–	–	–	265	5
Kirkidium knightii (J. Sowerby)	–	–	–	3	1	–
Leangella segmentum (Lindström)	–	9	–	–	–	–
Leptaena depressa (J. de C. Sowerby) and *Lepidoleptaena* sp.	–	5	4	165	85	26
Leptostrophia filosa (J. de C. Sowerby)	–	1	21	584	36	–
Lingula lata J. de C. Sowerby*	1	1	–	–	–	–
Lingula lewisii J. de C. Sowerby	–	19	7	54	19	3
Lingula n. sp.	–	10	–	–	–	–
Ludfordina pixis Kelly	–	192	–	–	–	–
Meristina obtusa (J. de C. Sowerby)	–	–	–	1	–	–
Mesopholidostrophia laevigata (J. de C. Sowerby)	–	34	69	1053	63	2
Nucleospira pisum (J. de C. Sowerby)	–	9	28	–	–	–
Orbiculoidea rugata (J. de C. Sowerby)	–	2	1	4	4	5
Parastrophinella sp.	35	133	–	–	–	–
Plagiorhyncha sp.	10	353	–	–	–	–
Protochonetes ludloviensis Muir-Wood	–	–	–	2	54	33
Protochonetes minimus (J. de C. Sowerby)	2	217	28	125	–	–
? *Protozeuga* sp.	–	87	3	–	–	–
Resserella sabrinae nunfieldensis Hurst	3	13	–	–	–	–
Resserella sp.	–	–	–	2	–	–
Rhynchospirina sp.	–	–	–	4	10	–
Salopina lunata (J. de C. Sowerby)	–	–	–	–	3	–
'*Schuchertella*' sp.	–	14	10	90	4	–
Shagamella ludloviensis Boucot & Harper*	–	145	3152	724	73	5
Shaleria ornatella (Davidson)	–	–	–	41	17	4
Skenidioides lewisii (Davidson)	1	306	80	7	–	–
Sphaerirhynchia wilsoni (J. Sowerby)	–	–	34	1082	872	48
Strophonella euglypha (Hisinger)	–	27	13	493	20	3
indeterminate rhynchonellides	–	1	3	14	28	–
indeterminate spiriferides	–	–	6	95	13	3
indeterminate brachiopods	4	–	–	–	–	–
GASTROPODA						
Bellerophon baccatus Reed	–	2	–	–	–	–
Bembexia lloydii (J. de C. Sowerby)	–	20	14	34	51	4
Bucanopsis expansus (J. de C. Sowerby)	–	–	1	1	5	–
Cymbularia cf. *fastigata* (Lindström)	6	55	4	–	–	–
Euomphalus sp.	–	10	–	38	14	1
gastropod sp. A	2	3	–	–	–	–
gastropod sp. B	–	1	–	–	–	–
Leptozone striatissima (Salter)	–	21	8	21	33	–
Loxonema sinuosa (J. de C. Sowerby)	18	32	–	1	–	–
murchisoniacean sp. B	–	–	–	3	1	–
Oriostoma sp.	–	1	–	24	28	45
platyceratacean sp. A	–	–	–	1	–	–
pleurotomariacean sp. A	–	17	–	–	–	–
pleurotomariacean sp. B	1	11	–	–	–	–

Table 15 continued

Association	Go1	Go2	tr	Ml	lpSw	AC
Sinuspira stokei (Longstaff)	4	22	–	–	–	–
Sphenosphaera sp.	3	6	–	–	–	–
Temnodiscus salopiensis Reed	–	1	–	–	–	–
indeterminate bellerophontaceans	–	1	1	2	1	1
indeterminate high-spired gastropods	–	–	4	8	5	–
indeterminate gastropods	6	48	5	25	28	21
BIVALVIA						
Actinopteria sowerbyi (M'Coy)	–	2	–	20	7	–
bivalve sp. A	–	–	1	2	–	–
bivalve sp. B	1	1	–	–	–	–
bivalve sp. C	–	–	–	2	2	–
bivalve sp. F	–	–	–	5	1	–
Buchiola sp.*	3	–	–	–	–	–
Butovicella migrans (Barrande)*	13	9	–	–	–	–
Cardiola interrupta (J. de C. Sowerby)*	10	21	4	–	1	–
Conocardium sp.	–	1	1	–	–	–
Cypricardinia subplanulata Reed	–	–	2	39	8	–
'*Cyrtodonta*' *perovalis* (Salter)	–	9	7	2	2	–
cyrtodontid sp. A	–	–	–	1	–	–
Dualina striata (J. de C. Sowerby)*	6	12	–	–	–	–
Goniophora cymbaeformis (J. de C. Sowerby)	–	12	12	8	7	–
grammysid sp. A	–	35	9	–	–	–
Grammysioidea sp.	–	–	–	2	–	–
Leptodesma ampliata (Phillips)	–	2	1	1	–	–
Modiolopsis consors Reed	–	4	3	–	–	–
Modiolopsis solenoides (J. de C. Sowerby)	–	2	2	2	–	–
modiomorphid sp. A	–	–	1	–	3	–
modiomorphid sp. B	–	–	1	2	2	–
modiomorphid sp. C	–	–	1	1	–	–
modiomorphid sp. D	–	9	–	–	–	–
modiomorphid sp. E	–	3	8	–	–	–
modiomorphid sp. F	–	–	1	–	–	–
Mytilarca siluriana Reed	–	13	14	8	6	–
Nuculites antiqua (J. de C. Sowerby)	–	–	–	9	10	–
Nuculites pseudodeltoideus Reed	–	4	1	–	–	–
Nuculites woolhopensis Reed	9	109	9	–	–	–
Orthonota rigida (J. de C. Sowerby)	–	5	5	11	5	–
Orthonota sp. A	–	–	1	–	–	–
Palaeopecten danbyi (M'Coy)	–	–	3	5	1	–
'*Paracyclas*' *insueta* Reed	–	–	2	5	2	–
Praectenodonta ludensis (Reed)	1	8	2	–	–	–
Praenucula sp.	9	91	1	–	–	–
Pteronitella retroflexa (Wahlenberg)	–	–	–	3	–	3
Ptychopteria tenuistriata (M'Coy)	–	–	–	4	1	–
Sedgwickia amygdalina (J. de C. Sowerby)	–	–	–	5	5	–
Similodonta sp.	–	–	1	4	–	–
Slava fibrosa (J. de C. Sowerby)*	3	–	–	–	–	–
indeterminate pteriaceans	–	2	4	–	–	–
indeterminate bivalves	7	32	31	33	11	2
CEPHALOPODA						
'*Cyrtoceras*' *laevis* (J. de C. Sowerby)	–	16	1	–	–	–
Cyrtocycloceras tenuiannulatum (M'Coy)	1	7	1	6	1	–

Table 15 continued

Association	Go1	Go2	tr	M1	lpSw	AC
Cyrtocycloceras tracheale (J. de C. Sowerby)	6	15	1	–	5	1
Dawsonoceras annulatum (J. Sowerby)	–	2	–	–	–	–
Kionoceras caniculatum (J. de C. Sowerby)	4	2	2	1	6	4
Kionoceras sp. B	–	2	2	6	2	–
'*Orthoceras*' *dimidiatum* (J. de C. Sowerby)*	×	×	3	–	–	–
'*Orthoceras*' *gregarium* (J. de C. Sowerby)*	×	×	3	2	–	–
Phragmoceras sp.	–	–	–	1	–	–
? *Polygrammoceras bullatum* (J. de C. Sowerby)	–	5	–	–	–	–
indeterminate cephalopods	–	28	12	12	11	3
TRILOBITA						
Calymene sp.	–	3	4	25	1	–
Dalmanites myops (König)	25	254	33	73	40	4
Encrinurus n. sp.	–	–	–	35	3	–
Hemiarges sp.	–	–	–	1	–	–
Leonaspis coronata (Salter)	3	21	–	–	–	–
Otarion megalops (M'Coy)	1	–	–	8	1	–
Phacops sp.	–	4	–	–	–	–
Proetus astringens Owens	–	6	6	61	4	–
Proetus obconicus (Lindström)	–	–	–	5	–	–
Raphiophorus parvulus (Forbes)	2	4	–	–	–	–
indeterminate trilobites	–	1	1	3	5	1
PHYLLOCARIDA						
Ceratiocaris sp.	–	1	–	–	–	–
INCERTAE SEDIS						
Conularia sp.	–	–	–	1	–	–
Cornulites serpularius Schlotheim	–	–	2	11	1	2
Hyolithes forbesi (Sharpe)	–	15	8	–	–	–
Tentaculites tenuis (J. de C. Sowerby)	–	–	–	26	2	1
TOTAL INDIVIDUALS	192	5420	1426	8472	4095	833
TOTAL SAMPLES	18	48	21	90	37	11

Table 16 Cumulative faunal content for samples assigned to the following associations: upSw – upper phase of *S. wilsoni*; So – *S. ornatella*; Pl – *P. ludloviensis*. Within each association, samples have been grouped into two taphonomic categories: d – disturbed neighbourhood assemblages; t – transported assemblages. Species marked with an asterisk are considered to be pelagic, and their numbers are not included in the final total of individuals

Association	upSw	upSw	So	So	Pl	Pl
Taphonomic category	t	d	t	d	t	d
ANTHOZOA						
solitary trochoid coral	–	2	–	–	–	–
BRYOZOA	47	59	7	32	49	152
BRACHIOPODA						
Atrypa reticularis (Linnaeus)	55	35	21	122	–	8
'*Camarotoechia*' *nucula* (J. de C. Sowerby)	412	579	43	170	367	1091

Table 16 continued

Association Taphonomic category	upSw t	upSw d	So t	So d	Pl t	Pl d
Craniops implicata (J. de C. Sowerby)	1	327	–	–	4	5
Dayia navicula (J. de C. Sowerby)	158	30	1	8	2	26
Dolerorthis sp.	1	–	–	–	–	–
Eospirifer radiatus (J. de C. Sowerby)	–	3	–	–	–	–
Howellella elegans (Muir-Wood)	331	200	24	35	19	34
Hyattidina canalis (J. de C. Sowerby)	353	108	5	6	–	–
Isorthis clivosa Walmsley	–	–	71	78	2	16
Isorthis orbicularis (J. de C. Sowerby)	172	274	–	5	–	–
Leptaena depressa (J. de C. Sowerby) and *Lepidoleptaena* sp.	–	4	13	141	1	1
Leptostrophia filosa (J. de C. Sowerby)	18	1	1	6	–	–
Lingula lewisii J. de C. Sowerby	–	9	1	6	–	15
Orbiculoidea rugata (J. de C. Sowerby)	1	7	1	4	10	24
Protochonetes ludloviensis Muir-Wood	220	173	22	18	1484	1900
Salopina lunata (J. de C. Sowerby)	248	179	102	22	800	366
Shagamella ludloviensis Boucot & Harper*	369	112	5	20	–	–
Shaleria ornatella (Davidson)	42	10	269	130	–	13
Sphaerirhynchia wilsoni (J. Sowerby)	467	192	–	7	–	3
indeterminate spiriferides	–	12	–	–	–	–
GASTROPODA						
Bembexia lloydii (J. de C. Sowerby)	1	4	–	–	–	2
Bucanopsis expansus (J. de C. Sowerby)	1	1	–	1	4	39
Cyclonema corallii (J. de C. Sowerby)	7	10	–	–	5	17
Euomphalus sp.	–	1	–	–	–	–
murchisoniacean sp. A	–	–	–	1	–	–
Oriostoma sp.	–	1	–	–	–	–
platyceratacean sp. A	–	1	–	2	–	3
platyceratacean sp. B	–	–	1	–	–	2
indeterminate bellerophontaceans	1	1	–	–	–	–
indeterminate high-spired gastropods	1	1	–	2	2	9
indeterminate gastropods	11	7	–	–	3	3
BIVALVIA						
Actinopteria sowerbyi (M'Coy)	–	1	–	2	–	–
bivalve sp. D	2	–	–	–	–	–
bivalve sp. E	–	1	–	–	–	1
Cardiola interrupta (J. de C. Sowerby)*	1	1	–	2	–	2
Conocardium sp.	–	1	–	–	1	–
Cypricardinia subplanulata Reed	–	–	–	5	–	–
Cypricardinia sp. A	–	–	–	–	–	1
Dualina striata (J. de C. Sowerby)*	–	–	–	–	–	1
Goniophora cymbaeformis (J. de C. Sowerby)	2	6	–	3	6	39
grammysid sp. B	–	–	–	–	–	1
Grammysioidea sp.	–	–	–	2	–	2
Modiolopsis complanata (J. de C. Sowerby)	–	1	–	–	–	1
modiomorphid sp. A	–	1	–	3	–	6
Mytilarca siluriana Reed	–	–	–	1	–	–
Nuculites antiqua (J. de C. Sowerby)	5	11	6	2	12	89
Orthonota rigida (J. de C. Sowerby)	–	4	–	2	–	–
Palaeopecten danbyi (M'Coy)	1	–	–	1	–	1
'*Paracyclas*' *insueta* Reed	5	16	2	6	3	7
Pteronitella retroflexa (Wahlenberg)	3	9	4	11	2	33

Table 16 continued

Association Taphonomic category	upSw t	upSw d	So t	So d	Pl t	Pl d
Ptychopteria tenuistriata (M'Coy)	5	8	3	10	3	66
Sedgwickia amygdalina (J. de C. Sowerby)	3	33	9	16	18	165
Similodonta sp.	–	–	–	1	–	–
indeterminate bivalves	6	8	3	3	4	12
CEPHALOPODA						
Ascoceras vermiforme Blake	–	–	–	–	–	2
Cyrtocycloceras tracheale (J. de C. Sowerby)	1	–	1	–	2	5
Kionoceras caniculatum (J. de C. Sowerby)	–	–	1	–	–	1
indeterminate cephalopods	3	8	–	1	28	63
TRILOBITA						
Acastella spinosa (Salter)	–	–	–	1	–	1
Calymene neointermedia (R. & E. Richter)	–	–	1	1	–	–
Calymene sp.	1	–	–	–	–	–
Encrinurus stubblefieldi Tripp	–	–	–	2	–	2
Homalonotus knightii (König)	–	–	–	–	–	2
Proetus obconicus (Lindström)	–	1	1	3	–	–
indeterminate trilobites	1	1	1	–	1	2
PHYLLOCARIDA						
Ceratiocaris sp.	–	–	–	–	1	3
EURYPTERIDA						
eurypterid fragment	–	–	–	–	–	1
INCERTAE SEDIS						
Cornulites serpularius Schlotheim	6	2	3	3	8	11
Serpulites longissimus J. de C. Sowerby	–	1	–	–	2	30
Tentaculites tenuis J. de C. Sowerby	15	8	2	4	–	–
TOTAL INDIVIDUALS	2607	2352	619	879	2843	4276
TOTAL SAMPLES	36	38	5	11	29	58

Table 17 An example of the *Glassia obovata* Association in the mudstone facies of the Middle Elton Beds. The samples are from section 1E, Upper Millichope, and provide part of the data upon which Fig. 22 is based. Species marked with an asterisk are considered to be pelagic, and their numbers are not included in the final total of individuals. Authorship of specific names can be found in Table 15

Sample number	1E8	1E9	1E10	1E11	1E12	1E13	1E14	1E15	1E16
cm above base of section	877	812	732	636	546	421	191	102	0
Vertical thickness of sample (cm)	23	12	10	15	15	5	20	8	12
ANTHOZOA									
solitary trochoid coral	–	–	–	1	–	–	–	–	–
syringoporid	–	–	–	–	1	–	–	–	–
BRACHIOPODA									
*Aegiria grayi**	1	725	5800	1880	1580	86	76	215	26
Amphistrophia funiculata	–	–	–	1	–	–	–	–	–

Table 17 continued

Sample number	1E8	1E9	1E10	1E11	1E12	1E13	1E14	1E15	1E16
cm above base of section	877	812	732	636	546	421	191	102	0
Vertical thickness of sample (cm)	23	12	10	15	15	5	20	8	12
Craniops implicata	–	–	3	160	2	3	–	62	2
Dicoelosia biloba	–	–	–	–	–	–	–	–	1
Eospirifer radiatus	–	–	–	–	–	–	–	–	2
Glassia obovata	8	–	5	5	3	–	3	–	4
Howellella elegans	–	–	–	–	–	1	–	–	–
Isorthis clivosa	29	4	2	4	7	25	14	9	21
Leangella segmentum	–	1	–	7	–	–	–	–	–
Lingula n. sp.	–	–	–	–	–	–	1	–	3
Ludfordina pixis	–	–	–	–	–	65	–	–	60
Mesopholidostrophia laevigata	–	–	–	2	2	5	–	–	11
Parastrophinella sp.	12	12	22	4	10	29	3	4	2
Plagiorhyncha sp.	4	12	29	9	36	4	7	13	7
Protochonetes minimus	–	12	12	4	9	4	18	12	10
? *Protozeuga* sp.	1	–	–	–	–	–	2	1	–
Resserella sabrinae nunfieldensis	3	–	2	2	–	–	1	–	–
Skenidioides lewisii	1	6	3	3	1	5	3	–	65
GASTROPODA									
Cymbularia cf. *fastigata*	2	–	–	4	–	–	–	–	–
Euomphalus sp.	–	–	1	4	–	–	–	–	–
gastropod sp. B	–	–	–	1	–	–	–	–	–
Leptozone striatissima	–	–	2	3	–	–	–	–	2
Loxonema sinuosa	1	–	–	–	–	–	–	3	–
pleurotomariacean sp. B	4	–	–	–	–	–	–	–	–
Sinuspira stokei	–	–	–	2	1	–	1	–	–
Temnodiscus salopiensis	–	–	–	–	–	1	–	–	–
BIVALVIA									
bivalve sp. B	–	–	–	–	1	–	–	–	–
*Butovicella migrans**	–	–	2	–	–	–	1	1	–
*Cardiola interrupta**	–	1	–	1	–	1	–	–	1
'*Cyrtodonta*' *perovalis*	–	1	–	–	–	–	–	–	–
*Dualina striata**	1	–	–	–	–	–	–	1	1
Goniophora cymbaeformis	–	–	–	–	–	–	–	–	1
grammysid sp. A	2	1	1	3	–	–	3	4	2
Leptodesma ampliata	–	–	1	–	–	–	–	–	–
modiomorphid sp. D	–	–	1	–	–	–	–	–	1
Mytilarca siluriana	–	–	–	–	–	–	–	2	1
Nuculites pseudodeltoideus	–	–	–	–	–	–	–	–	1
Nuculites woolhopensis	–	–	–	1	3	–	–	–	1
Praectenodonta ludensis	–	1	1	–	–	–	–	–	1
Praenucula sp.	7	2	3	1	–	–	3	2	–
indeterminate pteriaceans	–	–	1	–	–	–	–	1	–
indeterminate bivalves	–	1	–	3	1	1	2	–	–
CEPHALOPODA									
'*Cyrtoceras*' *laevis*	3	1	–	–	–	–	–	3	–
Cyrtocycloceras tenuiannulatum	–	–	–	–	–	–	–	–	1
Cyrtocycloceras tracheale	–	–	1	1	–	–	–	–	1
Dawsonoceras annulatum	1	–	–	–	1	–	–	–	–
Kionoceras caniculatum	–	–	–	–	1	–	–	–	–

Table 17 continued

Sample number	1E8	1E9	1E10	1E11	1E12	1E13	1E14	1E15	1E16
cm above base of section	877	812	732	636	546	421	191	102	0
Vertical thickness of sample (cm)	23	12	10	15	15	5	20	8	12
'*Orthoceras*' *dimidiatum**	4	–	6	–	–	–	–	7	6
'*Orthoceras*' *gregarium**	2	5	9	1	7	1	14	8	5
? *Polygrammoceras bullatum*	1	–	–	–	–	–	–	–	–
indeterminate cephalopods*	3	1	–	2	2	3	1	–	1
TRILOBITA									
Calymene sp.	–	–	–	1	–	2	–	–	–
Dalmanites myops	10	4	5	9	5	7	6	8	3
Leonaspis coronata	–	–	–	–	1	1	–	1	–
Raphiophorus parvulus	–	1	1	1	–	–	–	–	–
PHYLLOCARIDA									
Ceratiocaris sp.	–	–	–	–	–	–	1	–	–
INCERTAE SEDIS									
Hyolithes forbesi (Sharpe)	–	–	–	–	1	–	–	1	–
TOTAL INDIVIDUALS	88	59	96	236	86	153	68	126	203

Table 18 An example of the *Mesopholidostrophia laevigata* Association in the calcisiltite facies of the Lower Bringewood Beds. The samples are from section 4B, Ledbury, and provide part of the data upon which Fig. 19 is based. Species marked with an asterisk are considered to be pelagic, and their numbers are not included in the final total of individuals. Authorship of specific names can be found in Table 15

Sample number	4B18	4B19	4B20	4B21	4B23	4B24	4B25	4B26	4B27
cm above base of section	4695	4545	4353	4213	3739	3633	3528	3299	2480
Vertical thickness of sample (cm)	40	20	12	15	56	7	10	16	15
ANTHOZOA									
solitary trochoid corals	–	8	–	1	–	–	–	–	2
BRYOZOA	6	11	8	1	5	5	3	3	11
BRACHIOPODA									
Amphistrophia funiculata	5	4	2	1	2	–	2	1	2
Atrypa reticularis	5	3	3	3	57	7	24	20	5
'*Camarotoechia*' *nucula*	3	2	–	4	4	–	–	–	–
Craniops implicata	–	2	1	–	–	1	–	–	–
Cyrtia exporrecta	1	–	–	–	–	–	–	–	–
Dalejina hybrida	1	1	–	1	1	–	–	–	–
Eospirifer radiatus	–	1	–	3	–	–	2	–	–
Gypidula lata	–	–	–	32	2	–	–	2	7
Howellella elegans	14	–	–	–	1	1	–	2	–
Isorthis clivosa	49	13	12	14	40	4	14	9	2

Table 18 continued

Sample number	4B18	4B19	4B20	4B21	4B23	4B24	4B25	4B26	4B27
cm above base of section	4695	4545	4353	4213	3739	3633	3528	3299	2480
Vertical thickness of sample (cm)	40	20	12	15	56	7	10	16	15
Leptaena depressa and *Lepidoleptaena* sp.	8	1	–	3	–	–	–	1	1
Leptostrophia filosa	19	2	–	82	9	–	2	1	1
Lingula lewisii	2	–	3	–	1	–	–	–	–
Mesopholidostrophia laevigata	8	1	1	12	8	2	8	7	2
Orbiculoidea rugata	–	–	–	–	–	1	–	–	–
Protochonetes minimus	–	–	–	4	–	–	1	–	–
'*Schuchertella*' sp.	–	3	1	1	–	–	–	–	–
*Shagamella ludloviensis**	1	2	–	–	2	64	4	–	3
Shaleria ornatella	–	1	–	1	–	–	–	–	–
Sphaerirhynchia wilsoni	47	8	5	4	55	2	6	11	19
Strophonella euglypha	–	4	–	5	–	–	–	1	2
indeterminate spiriferides	–	–	–	–	15	–	3	–	3
Gastropoda									
Bembexia lloydii	–	–	–	6	2	–	–	1	1
Euomphalus sp.	1	–	1	–	1	–	–	–	–
Leptozone striatissima	–	1	1	1	–	–	–	–	1
Loxonema sinuosa	–	–	1	–	–	–	–	–	–
Oriostoma sp.	–	–	–	–	–	–	–	–	2
indeterminate bellerophontacean	–	1	–	–	–	–	–	–	–
indeterminate gastropods	–	–	–	2	–	–	–	–	–
Bivalvia									
Actinopteria sowerbyi	–	1	–	–	–	–	1	–	–
bivalve sp. A	–	–	–	–	–	1	–	1	–
bivalve sp. C	–	–	–	–	1	–	–	–	–
bivalve sp. F	–	1	–	–	2	–	–	–	1
Cypricardinia subplanulata	–	–	–	–	1	–	1	–	–
'*Cyrtodonta*' *perovalis*	–	–	1	–	–	–	–	–	–
modiomorphid sp. C	–	–	1	–	–	–	–	–	–
Orthonota rigida	–	–	–	1	–	–	–	–	–
'*Paracyclas*' *insueta*	–	–	–	–	1	–	–	1	–
Ptychopteria tenuistriata	–	–	–	–	–	–	–	1	–
Sedwickia amygdalina	–	1	–	3	–	–	–	–	–
indeterminate bivalves	1	1	4	–	4	–	1	2	–
Cephalopoda									
Cyrtocycloceras tenuiannulatum	–	–	1	–	1	–	–	–	–
Kionoceras sp. B	1	–	–	–	–	–	–	–	–
indeterminate cephalopods	–	–	1	–	–	–	–	1	–
Trilobita									
Calymene sp.	–	1	–	–	1	–	–	–	1
Dalmanites myops	1	–	1	–	4	–	1	–	1
Encrinurus n. sp.	1	–	1	1	–	1	–	–	–
Proetus astrigens	–	–	–	–	3	–	–	–	2
Total individuals	173	72	49	186	221	25	69	65	66

Table 19 Examples of the upper phase of the *Sphaerirhynchia wilsoni* Association (upSw) and *Shaleria ornatella* Association (So) in the coquinoid siltstone facies of the Lower and Upper Leintwardine Beds. The samples are from section 4A, north of Ledbury, and provide part of the data upon which Fig. 18 is based. Species marked with an asterisk are not included in the final total of individuals; authorship of specific names can be found in Table 16. For taphonomic category of samples: d – disturbed neighbourhood assemblage; t – transported assemblage

Sample number	4A27	4A28	4A29	4A30	4A31	4A32	4A33	4A34	4A35
Association	So	So	So	upSw	upSw	upSw	upSw	upSw	upSw
Stratigraphic unit	ULB	ULB	ULB	LLB	LLB	LLB	LLB	LLB	LLB
cm above base of section	4437	4377	4277	4257	4144	4056	3959	3861	3751
Vertical thickness of sample (cm)	6	9	7	8	8	8	2	2	6
Taphonomic category	d	d+t	d	d	t	t	t	d	d
BRYOZOA	–	2	1	–	–	–	1	–	2
BRACHIOPODA									
Atrypa reticularis	–	12	40	–	–	–	–	–	–
'*Camarotoechia*' *nucula*	10	21	74	17	20	4	9	13	11
Dayia navicula	–	–	–	–	–	–	1	–	–
Howellella elegans	2	14	27	–	3	3	1	–	5
Hyattidina canalis	–	2	6	–	4	3	2	6	6
Isorthis clivosa	1	63	–	–	–	–	–	–	–
Isorthis orbicularis	–	–	–	–	1	3	6	1	1
Leptaena depressa and *Lepidoleptaena* sp.	17	2	52	–	–	–	–	–	–
Lingula lewisii	–	2	1	–	–	–	–	–	–
Protochonetes ludloviensis	7	4	4	3	10	26	6	4	13
Salopina lunata	1	5	12	23	5	3	4	2	5
Shaleria ornatella	–	164	5	–	–	–	–	–	–
Sphaerirhynchia wilsoni	–	–	7	–	2	8	20	20	6
GASTROPODA									
Bucanopsis expansus	–	–	–	–	1	–	–	–	–
Cyclonema corallii	–	–	–	2	1	–	–	–	–
indeterminate gastropods	–	–	–	–	–	–	1	–	1
BIVALVIA									
Actinopteria sowerbyi	–	–	2	–	–	–	–	–	–
bivalve sp. D	–	–	–	–	2	–	–	–	–
*Cardiola interrupta**	–	–	–	–	–	–	–	1	–
Cypricardinia subplanulata	–	–	2	–	–	–	–	–	–
Goniophora cymbaeformis	1	–	1	–	–	–	–	–	–
modiomorphid sp. A	1	–	1	–	–	–	–	–	–
'*Paracyclas*' *insueta*	1	–	3	–	–	–	1	–	–
Pteronitella retroflexa	4	4	–	–	–	–	–	–	1
Ptychopteria tenuistriata	1	3	2	1	–	–	1	–	–
Sedgwickia amygdalina	1	2	4	13	–	–	1	5	1
Similodonta sp.	–	–	1	–	–	–	–	–	–
CEPHALOPODA	1	–	–	1	–	–	–	–	–
TRILOBITA									
Acastella spinosa	1	–	–	–	–	–	–	–	–
Calymene neointermedia	–	1	–	–	–	–	–	–	–
Proetus obconicus	–	–	1	–	–	–	–	–	–

Table 19 continued

Sample number	4A27	4A28	4A29	4A30	4A31	4A32	4A33	4A34	4A35
Association	So	So	So	upSw	upSw	upSw	upSw	upSw	upSw
Stratigraphic unit	ULB	ULB	ULB	LLB	LLB	LLB	LLB	LLB	LLB
cm above base of section	4437	4377	4277	4257	4144	4056	3959	3861	3751
Vertical thickness of sample (cm)	6	9	7	8	8	8	2	2	6
Taphonomic category	d	d+t	d	d	t	t	t	d	d
INCERTAE SEDIS									
Cornulites serpularius	–	1	–	–	1	–	–	–	–
Tentaculites tenuis	–	2	2	–	–	–	–	1	1
TOTAL INDIVIDUALS	49	304	248	60	50	50	54	52	53

Table 20 An example of the *Protochonetes ludloviensis* Association in the coquinoid siltstone facies of the Lower Whitcliffe Beds. The samples are from section 2C, Ludlow, and provide part of the data upon which Fig. 16 is based. All samples are disturbed neighbourhood assemblages. Authorship of specific names can be found in Table 16

Sample number	2C1	2C2	2C3	2C4	2C5	2C6	2C7	2C8	2C9
cm above base of section	2349	2240	2134	1995	1859	1672	1520	1421	1168
Vertical thickness of sample (cm)	7	7	6	7	15	15	12	11	14
BRYOZOA	1	–	1	–	3	1	16	4	2
BRACHIOPODA									
Atrypa reticularis	–	–	–	–	–	–	–	2	–
'*Camarotoechia*' *nucula*	8	7	1	4	21	5	25	28	28
Craniops implicata	–	–	1	–	–	–	1	–	–
Dayia navicula	–	–	–	–	–	3	–	1	1
Isorthis clivosa	–	–	–	–	–	–	–	4	–
Lepidoleptaena sp.	–	–	–	–	–	–	–	1	–
Lingula lewisii	–	–	–	1	–	1	–	–	–
Orbiculoidea rugata	–	–	–	–	1	–	–	–	–
Protochonetes ludloviensis	89	39	44	39	6	22	2	3	10
Salopina lunata	1	3	1	2	5	9	–	1	2
GASTROPODA									
Bembexia lloydii	–	–	–	–	–	–	–	1	–
Bucanopsis expansus	1	–	1	1	2	–	1	–	–
platyceratacean sp. A	–	–	–	–	–	–	2	1	–
platyceratacean sp. B	–	–	–	–	–	–	1	–	–
indet. high-spired gastropods	–	–	–	–	–	–	4	1	–
BIVALVIA									
*Dualina striata**	–	–	–	–	–	1	–	–	–
Goniophora cymbaeformis	–	–	–	–	–	–	–	1	–
Grammysioidea sp.	–	–	–	–	–	–	–	1	–
Nuculites antiqua	–	–	–	–	1	2	–	–	–
Pteronitella retroflexa	–	–	–	1	–	–	–	–	–
Ptychopteria tenuistriata	–	1	–	1	2	1	3	–	–

Table 20 continued

Sample number	2C1	2C2	2C3	2C4	2C5	2C6	2C7	2C8	2C9
cm above base of section	2349	2240	2134	1995	1859	1672	1520	1421	1168
Vertical thickness of sample (cm)	7	7	6	7	15	15	12	11	14
Sedgwickia amygdalina	–	–	1	1	9	6	–	1	3
indeterminate bivalve	–	–	–	–	–	–	–	1	–
CEPHALOPODA									
Ascoceras vermiforme	–	–	–	2	–	–	–	–	–
Cyrtocycloceras tracheale	1	–	–	–	–	–	–	1	–
Kionoceras caniculatum	–	–	–	–	–	–	1	–	–
indeterminate cephalopods	–	1	–	1	4	–	1	1	3
TRILOBITA									
Encrinurus stubblefieldi	–	–	–	–	–	–	1	1	–
indeterminate trilobite	–	–	–	–	–	–	–	–	1
TOTAL INDIVIDUALS	101	51	50	53	54	50	58	54	50

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The ammonites of the English Chalk Rock (Upper Turonian)

C. W. Wright

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Synopsis

The English Chalk Rock fauna of ammonites (Upper Cretaceous, Upper Turonian) is described as an aid to international correlation. It comprises 28 species and subspecies referred to 15 genera. Five new species (*Anisoceras reidi*, *Allocrioceras strangulatum*, *Scaphites diana*, *Otoscaphites reidi* and *Lewesiceras woodi*) and 2 new subspecies (*Scaphites geinitzii laevior* and *S. lamberti doylei*) are described. Lectotypes are designated of *Scaphites geinitzii* d'Orbigny, *S. g. intermedius* Scupin, *S. fritschi* Grossouvre [= *S. auritus* Fritsch, *non* Schlüter] and *Puzosia curvatisulcata* Chatwin & Withers. *Pseudopuzosia* Spath is placed in the synonymy of *Pseudojacobites* Spath.

Introduction

This paper comprises a full description of the ammonite component of the fauna of the Upper Turonian Chalk Rock of southern England, together with some conclusions for correlation. The fauna includes a number of wide-ranging ammonite species and, since they occur together in England in beds representing a relatively short period of time, the fauna is of particular importance as a standard of comparison in a stage in which few abundant ammonite faunas are known.

The individual study of which this paper describes some of the results has been largely overtaken by the International Geological Correlation Programme Project on Mid-Cretaceous Events and the paper is therefore offered in the context of that project.

The Chalk Rock

Above the Cenomanian the English Chalk ceases in general to contain many ammonites and it is only at a few narrow horizons that they are at all common. The best-known of these is the Chalk Rock. It is a variable composite hardground or series of hardgrounds (Kennedy & Garrison 1975 and references therein) up to about 4 m thick, but generally less, occurring in the lower part of the *Holaster planus* Zone, the highest of the three conventional zones of the English Turonian chalk. The upper surface (where it comprises a single bed) and the top of individual hardgrounds (where separate) are irregular, and generally have included in them or immediately above them phosphatized cemented chalk pebbles, often green-coated, and phosphatized fossils. Similar fossils, normally less well preserved and less abundant, may be found lower in the hardgrounds. The fauna is large and varied; its most characteristic elements are lithistid and hexactinellid sponges and aragonitic molluscs – scaphopods, gastropods, bivalves and cephalopods. Woods (1896–97) described and figured many of them and Billinghurst (1927) described further species of ammonites. In recent years much collecting has been done, particularly at Billinghurst's locality of Hill End Farm, Hitch Wood near Hitchin, at Reed near Royston and at Kensworth near Luton. A good many new forms have come to light.

Although specimens of ammonites have been collected at various levels in the series of hardgrounds at different localities there is no significant difference in the lists from place to place apart from the abundance of *Baculites undulatus* at Reed and Kensworth and its absence elsewhere. It is therefore reasonable to treat the fauna as a single one, occupying part of the lower part of the *Holaster planus* Zone.

The Chalk Rock occurs in East Anglia and the south Midlands, extending as far west as north Dorset and Wiltshire. Outside this area there may be incipient hardgrounds or beds of nodular chalk that yield the Chalk Rock fauna. Elsewhere specimens of the aragonitic mollusca may occasionally be found in normal chalk of the *Holaster planus* Zone. In Yorkshire several cases are known (Wright 1935) of patches of chalk containing abundant aragonitic gastropods and bivalves apparently protected from dissolution by large ammonite shells that lay above them. It can only be assumed therefore that elements of the Chalk Rock fauna occurred more widely and persistently than in the special conditions under which the hardgrounds were formed.

Systematic descriptions

The following abbreviations are used.

BM	British Museum (Natural History)
coll.	collected by, or collection of
GSM	Geological Survey Museum of the Institute of Geological Sciences
GSP	Geological Survey, Pretoria, South Africa
IGS	Institute of Geological Sciences
MMH	Mineralogical Museum, Copenhagen
SM	Sedgwick Museum, Cambridge
WW	C. W. & E. V. Wright collection

Superfamily **TURRILITACEAE** Meek, 1876

Wiedmann (1962 : 179; 1969; 1973) has published successive revisions of the classification of Cretaceous heteromorphs, mainly in contrast with that adopted in the *Treatise on Invertebrate Paleontology* (Wright 1957*b*). A few points, relevant to the present work, are discussed here.

Wiedmann rejects the separation at superfamily level of the Turrilitaceae from the Ancylocerataceae. However, even if, as is probable, the earliest families assigned to the Turrilitaceae (Anisoceratidae and Hamitidae) were derived from one or more ancyloceratine ancestors, the Turrilitaceae represent a renewed radiation based primarily on bifid sutural lobes, in contrast with the trend to trifid lobes in most stocks of Ancylocerataceae.

Wiedmann included in an enlarged family Baculitidae not only the Hamitinae, Baculitinae and Polyptychoceratinae but also Ptychoceratinae; moreover his Baculitinae embraced the wholly Lower Cretaceous group of Bochianitinae. There is in fact no good evidence to contradict Spath's (1941 : 659) view that the Baculitidae were derived, by way of *Lechites*, from straightening members of *Hamites*; they constitute a group starting with and retaining bifid lateral lobes. On the other hand the Bochianitidae start (in late Jurassic) and end with trifid lateral lobes.

As to the taxonomic level of the hamitids and baculitids, although the sutures are generally similar the remainder of the morphology is so distinct (with implications for the biology) that by normal ammonite standards family separation is wholly justifiable.

There is much to be said for Wiedmann's reduction of the Nostoceratidae and Diplomoceratidae to subfamilies of Turrilitidae, and this view is adopted here. The former include a wide range of late Upper Cretaceous loosely and tightly coiled forms, many of which closely resemble the

Middle Albian immediate precursors of *Turrilites* and its close allies. The subfamily Diplomoceratinae, on the other hand, comprises a mixed bag of more or less hamitoid presumed offshoots of the Nostoceratinae.

Family **HAMITIDAE** Meek, 1876

Genus *METAPTYCHOCERAS* Spath, 1926

TYPE SPECIES. *Ptychoceras smithi* Woods, 1896.

The genus comprises small forms, with more or less straight penultimate and final shafts closely pressed together and finely ribbed; the almost smooth, feebly constricted initial shaft is described below for the first time.

The type species was the only one referred to the genus by Spath and he gave no generic diagnosis. Thus it is not clear what he envisaged as the difference between this genus and *Hemiptychoceras* from the Upper Albian which he described the year before (Spath 1925 : 189). *Metaptychoceras* is diagnosed (Wright 1957*b* : L217) as 'small; much like *Hemiptychoceras* but has fine ribbing of *Stomohamites*', as opposed to *Hemiptychoceras* which has 'ribs as in *Hamites* except on 2nd bend where they tend to be scale-like, as in some *Euptychoceras*'.

Subsequently Wiedmann (1959 : 715) quoted *M. smithi* from his Spanish zone of *Fallotites* (*Ingridella*) *malladae*, the fifth from the base of seven zones into which he divided the Lower Turonian. A species of the genus has also been found in Colombia. Cobban & Scott (1972 : 45) described a new species *Hemiptychoceras reesidei* from the uppermost Cenomanian (*Sciponoceras gracile* horizon) Bridge Creek Limestone of Colorado and referred to 'a smaller but very closely related species' from the basal Turonian with *Watinoceras coloradoense* of South Dakota.

Reviewing all this material it seems that the distinction between *Hemiptychoceras* and *Metaptychoceras* is slight but real. The former is larger, more coarsely ribbed and with constrictions on the penultimate shaft and final bend. The latter is very small, finely ribbed and with no constrictions after the initial shaft. A decision whether these differences justify generic separation must await the discovery of more specimens of these rare forms.

Metaptychoceras smithi (Woods)

Pl. 1, figs 1, 2

1896 *Ptychoceras smithi* Woods : pl. 2, figs 1, 2.
1926 *Metaptychoceras smithi* (Woods) Spath : 81.
1959 *Metaptychoceras smithi* (Woods); Wiedmann : 715.

HOLOTYPE. SM B4098, from Cuckhamsley Knob.

DESCRIPTION. Small, with two slender, more or less straight and parallel, shafts followed by a closely adpressed hook; there was probably a minute initial coiled spire, but this has not yet been found. The recurved part of the hook is circular in section and rests in a rather deep groove in the dorsum of the shaft; there is a minute 'umbilicus' at the bend. The first shaft is smooth except for an occasional feeble oblique constriction and accompanying fold. Weak oblique ribs begin soon after the first bend and rapidly become radial, low, rounded and dense. In one specimen (BM C79653; Pl. 1, fig. 1) on the later part of the second bend and the beginning of the second shaft they are rursiradiate, sharp and distant; thereafter they are a little coarser, more distant and radial. In another specimen (BM C79658) the ribs have almost disappeared on the bend and only become strong on the latter part of the final shaft. Woods differentiates the species from *Hemiptychoceras gaultinum* (Pictet) by the absence of any coarsening of the ribs on the bend, but the ribbing in the later stages in *M. smithi* seems to be variable and detailed differences are probably unimportant. The suture consists of rather wide and splayed, moderately subdivided and very regularly bifid elements; the external lobe is a little less deep than the first lateral lobe.

OCCURRENCE. The species seems to be rare, but being small may sometimes pass unnoticed. Besides the holotype from Cuckhamsley (SM B4098) there is a specimen (SM B21326) from Lannock Farm, east of Hitchin. Hill End Farm Pit, Hitch Wood yielded to R. E. H. Reid two specimens more complete than the holotype and to R. G. Bromley the juvenile specimen here figured. A specimen was recorded from Burham, Kent by Dibley (1912 : 373).

Family **BACULITIDAE** Meek, 1876

Genus ***SCIPONOCERAS*** Hyatt, 1894

TYPE SPECIES. *Hamites baculoides* Mantell, 1822.

Sciponoceras appears first in the *dispar–perinflatum* Subzone of the uppermost Albian in England and France. These early forms are not yet well known, since only rather short fragments of internal casts have been found. They seem to be derived directly from a species of *Lechites*, such as *L. communis* Spath, by the almost complete loss of ribs and the strengthening of constrictions. Small fragments of similar forms are found in the early Cenomanian Glauconitic Marl of the Isle of Wight. They may be distinct from the type species, *S. baculoides* (Mantell), but well-characterized specimens have yet to be found.

The Chalk Marl of Sussex and the Isle of Wight has yielded fairly well preserved specimens similar to the type specimens of *S. baculoides* (Kennedy 1971 : pl. 2, figs 1–5), characterized by an oval whorl section, strong and fairly close constrictions with only the faintest of intermediate ribs, strong ventral ribbing just before the aperture and a dorsally-directed aperture with ventral sinus and lateral lappets. By the middle of the Cenomanian in England (the Dorset and Somerset basement beds, Kennedy's *Turrilites acutus* assemblage) there is a species differing from *S. baculoides* mainly in its aperture, which is oblique instead of slightly curved, has only feeble lateral lappets and has a ventral rostrum instead of sinus. In the uppermost Cenomanian with *Metoicoceras* in Europe and the United States occurs *S. gracile* (Shumard), with ribs that become very strong in adults. In the earliest Turonian there is, in England at least, a form which foreshadows the typical *S. bohemicum* described below.

S. bohemicum (Fritsch) retains marked constrictions and an aperture not very different from that of the Cenomanian type species; despite certain other features it can be fairly regarded as a *Sciponoceras*. It is accompanied, however, by an early form of true *Baculites*, also described below, and is probably the last *Sciponoceras*.

Sciponoceras bohemicum (Fritsch)

Pl. 1, figs 3–5; Pl. 7, figs 10, 12

1843 *Baculites anceps* Geinitz : 9.
1850 *Baculites baculoides* Geinitz : 122.
1872 *Baculites faujassi* Lamarck var. *bohemica* Fritsch : 49; pl. 13, figs 23–25, 29, 30.
1874 *Baculites baculoides* Geinitz; Geinitz : 195; pl. 35, figs 17–21.
1875 *Baculites bohemicus* Fritsch; Barrois : 403.
1876 *Baculites* cf. *bohemicus* Fritsch; Schlüter : 140; pl. 39, figs 1–5.
1893 *Baculites Faujassi* var. *bohemica* Fritsch & Schlönbach; Fritsch : 80, fig. 63.
1895 *Baculites Faujassi* var. *bohemica* Fritsch; Jahn : 133; pl. 8, fig. 8.
1896 *Baculites bohemicus* Fritsch & Schlönbach; Woods : 76; pl. 2, figs 9, 10.
1908 *Baculites* (*Lechites*) *Bohemicus* Fritsch & Schlönbach; Nowák : 348–350.
1927 *Cyrtochilus bohemicus* (Fritsch & Schlönbach) Billinghurst : 513.
1951 *Sciponoceras bohemicum* (Fritsch) Wright & Wright : 16.

LECTOTYPE. The original of Fritsch's 1872: pl. 13, fig. 25a, b, c, here designated.

DESCRIPTION. The shell increases very slowly in height and width; it is elliptical in section with the sides tending to become flattened with age.

	Dorsoventral diameter	Transverse diameter
BM C79497	5·5 mm	4 mm
BM C79496	12·5 mm	9·5 mm

The body chamber becomes somewhat triangular in section towards the aperture. During the camerate stage there are on internal casts rather frequent broad shallow constrictions at somewhat irregular intervals. In the early stages they are almost as strong on the dorsum as on the sides and venter, but the dorsal part weakens with age and in many individuals they become almost imperceptible on the inner third of the side. The constrictions run backwards at an angle of about 120° to the long axis of the shell, then curve forward a third of the way up the side to run obliquely at about 40° to the long axis as far as the venter, which they cross in a broad curve with a steep rear and a shallow forward slope. Between the constrictions there are in the early stages two or three low rounded ribs, distinct on the outer third and on the venter. Later they become flattened and indistinctly branched. On the body chamber the ribs are distinct also on the inner part of the sides where they branch from crescentic bullae which are low but perceptible, to strong. At this stage, in the absence of constrictions, the ornament is somewhat like that of the camerate part of contemporary *Baculites undulatus*. At the aperture the dorsum and in fact the whole shell curves inwards, the aperture being directed about 45° dorsally. There are no lappets or collars such as characterize the Cenomanian species of *Sciponoceras*, and the aperture is much like that of *S. gracile* (Shumard).

The suture has rather irregularly bifid elements. The first lateral (external) saddle is much higher than the next one and the umbilical lobe and internal saddle are markedly shorter than the other elements.

REMARKS. Although *S. bohemicum* has been frequently quoted in the literature and has been figured several times there is no satisfactory description of the species. The English Chalk material has yielded many fragments of internal moulds in hard phosphatized chalk which allow an accurate assessment of the ornament to be made. There is good agreement with Fritsch's clear figures and there can be no doubt of the identity of the English with the Czechoslovakian material.

AFFINITIES AND DIFFERENCES. *S. bohemicum* is in many respects close to the uppermost Cenomanian *S. gracile* (Shumard) from which it is probably derived. Typical *S. gracile* differ in having a somewhat less compressed whorl section, in their stronger, more evenly rounded ribs becoming very strong on the body chamber, and in their constrictions that are noticeably less distinct on the sides and dorsum and cross the venter more or less transversely. In *S. bohemicum*, by contrast, the ribs are flat and almost scale-like even on the body chamber; the constrictions are frequently obvious even on the dorsum and cross the venter in an even curve. Some American populations of *S. gracile*, though not those of the English south-west, show variation in the strength of ribs and constrictions and some individuals in their early stages may be difficult to distinguish from *S. bohemicum*.

Specimens from the English Melbourne Rock (e.g. WW 16137–40 from Buckland Limeworks, Surrey, and SM B91099 and B91100 from Folkestone, Kent) that are only slightly later than the uppermost Cenomanian *S. gracile* from Devon have ribbing closely resembling that of *S. bohemicum* and constrictions strong on the inner part of the sides and the dorsum. The only feature linking them with *S. gracile* is the transverse course of the constrictions on the venter. They should probably be treated as a subspecies of *S. bohemicum*.

The Lower and Middle Cenomanian *S. baculoides* (Mantell) has ribs shallow behind and steep in front. They thus resemble the scale-like ribs of *S. bohemicum* but are much stronger, prorsiradiate as they rise near the dorsum and distinctly recurved towards the venter.

From contemporary forms assignable to *Baculites*, *S. bohemicum* is readily distinguished by its frequent and well-marked constrictions, although body-chamber fragments may be difficult to identify.

OCCURRENCE. *S. bohemicum* is widespread and fairly common in both Chalk Rock and nodular facies of the *Holaster planus* Zone of south-eastern England, East Anglia and the midlands. It occurs in northern and central Europe at presumably the same horizon.

Genus *BACULITES* Lamarck, 1799

TYPE SPECIES. *B. vertebralis* Lamarck, 1801, subsequently designated by Meek (1876).

Baculites appears to have been derived from an Upper Turonian *Sciponoceras* by loss of constrictions and further simplification of the aperture. I have seen no undoubted *Baculites* earlier than *B. undulatus* described below. Poorly-preserved and crushed *Sciponoceras*, particularly fragments of body chambers, often look deceptively like *Baculites*.

Baculites undulatus d'Orbigny

Pl. 1, figs 6–8; Pl. 7, fig. 11

1850 *Baculites undulatus* d'Orbigny : 19 & 21, no. 21.
? 1872 *Baculites undulatus* d'Orbigny ?; Fritsch : 49.
1895 *Baculites* n. sp. Jahn : 136; pl. 8, fig. 8a–c.
1913 *Baculites undulatus* d'Orbigny; Roman & Mazeran : 11; pl. 4, figs 6–8.
1963 *Baculites undulatus* d'Orbigny; Matsumoto & Obata : 28; pl. 8, fig. 4; pl. 9, figs 1–5; pl. 11, figs 2, 3; text-figs 62–71.

DESCRIPTION. Whorl section elliptical, narrowing ventrally with increasing age. The low rounded ribs are rursiradiate dorsally at about 150° but bend forward and become prorsiradiate at about 45° on the ventral three-quarters of the shell, forming a more or less crescentic bulla at the bend. At first the ribs are mainly single but from a (major) diameter of about 10 mm they begin to branch irregularly at or above the bulla. On the body chamber the dorsal part of most ribs becomes weaker, so there can be seen only rounded and well-spaced bullae from which spring sheaves of six or more feeble ribs. The aperture is described from Japanese specimens by Matsumoto & Obata (1963 : 29). The largest fragment seen (Doyle coll. 662) has diameters of 26 and 20·5 mm.

AFFINITIES AND DIFFERENCES. *B. undulatus* is readily distinguished at the camerate stage from the contemporary *Sciponoceras bohemicum* by the absence of constrictions and by the finer and weaker but more numerous ribs. On the body chamber the well-spaced bullae and sheaves of fine secondary ribs are sufficiently characteristic. Although d'Orbigny's types of *B. undulatus*, as figured by Roman & Mazeran (1913), are only small fragments they clearly belong to the same species as the better-preserved English specimens. Presumably the Bohemian specimens described but not figured by Fritsch belong to the same form.

The next earliest true *Baculites* that have been described are Coniacian species from the Pacific (Japan and California), Africa and Europe. *Baculites brevicosta* Schlüter (Coniacian or Lower Santonian of northern Europe), the African and Pacific *C. boulei* Collignon and *B. capense* Woods, and the American *B. asper* all have far more distinct and prominent crescentic bullae than those of *B. undulatus*. There is, however, an intermediate group comprising *B. yokoyamai* Tokunaga & Shimizu, *B. besairiei* Collignon and *B. schenki* Matsumoto. Describing the Californian forms Matsumoto (1959) considered that *B. yokoyamai*, which occurs frequently in Japan in the Coniacian immediately above *Sciponoceras* aff. *bohemicum*, probably includes *B. besairei* Collignon from Madagascar. These forms appear to have feebler ornament than the present species but similar whorl section and suture. The closely allied *B. schenki* from California is more triangular in section and typically has more strongly tuberculate dorsolateral crescents on the ribs.

B. undulatus could also well have been the source of the Coniacian *Euhomaloceras incurvatum* (Dujardin), characterized by distant, large, round dorsolateral tubercles as well as by the curved body chamber.

OCCURRENCE. In England *B. undulatus* is known only from a few localities, Reed in Hertfordshire and Kensworth.

Family **ANISOCERATIDAE** Meek, 1876

Genus ***ANISOCERAS*** Pictet, 1854

TYPE SPECIES. *Anisoceras saussureanum* Pictet.

Anisoceras reidi sp. nov.

Fig. 1; Pl. 1, fig. 15

TYPES. The holotype is BM C79487 (WW, *ex* Reid coll.) from Hitch Wood; a paratype is GSM 117001 (trans. from St Albans City Museum, *ex* Morison coll.) from Luton Railway Cutting.

NAME. For Mr R. E. H. Reid.

DESCRIPTION. The section is compressed and the venter only slightly flattened; the height increases rather rapidly. The ribs are fairly dense, low and rounded, irregularly with and without ventrolateral spines, of which low flat bases alone appear on the internal mould. The ribs with tubercles are doubled across the venter. The ribs are slightly bowed forward at midflank and are thus weakly biconcave. First and second lateral saddles of the suture and lateral and umbilical lobes are basically bifid but the lobes are irregularly asymmetric (Fig. 1); indeed the lateral lobe in the holotype is obviously bifid on the left side but almost trifid on the right. The third lateral saddle is distinctly narrower than the others.

REMARKS. R. E. H. Reid collected a single specimen of what appears to be a true *Anisoceras*, although superficially it resembles some contemporary *Allocrioceras*. Hitherto *Anisoceras* has been only doubtfully represented above the Cenomanian and it is already rare in the uppermost part of that stage. Schlüter (1872) described and figured from the uppermost Turonian two species that belong to this family, *Ancyloceras paderbornense* (1872 : 97; pl. 30, figs. 1, 2) and *A. cuvieri* (1872 : 97; pl. 30, figs 3, 4). The former, though not typical of *Anisoceras*, may be referred provisionally to that genus; it differs from *A. reidi* by its lateral tubercles and less regular and more distant ventrolateral tubercles. *A. cuvieri* (Schlüter) is perhaps best referred to *Allocrioceras* (see below). Although like *Anisoceras reidi* it has no lateral tubercles, it has ventrolateral ones only on every fifth or sixth rib, which is more prominent than the rest; moreover the ribs are slightly sinuous and more prorsiradiate than in the present species. Most *Allocrioceras* are distinguishable by their sharper ribs and tubercles and simpler sutures. However, the two new species of *Allocrioceras* described below have in their later stages rounded ribs and septate tubercles that leave flat spine bases on the internal moulds as in *Anisoceras*; their sutures are also complex in

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Plate 1 × 1 (Figs 1–2, 4–5 × 2)

Metaptychoceras smithi (Woods) (p. 284). Hitch Wood.
Fig. 1. Coll. R. E. H. Reid. BM C79653, × 2. Fig. 2. R. G. Bromley coll. C.146, × 2.

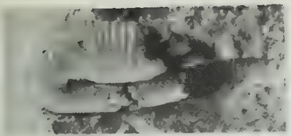
Sciponoceras bohemicum (Fritsch) (p. 285). Hitch Wood.
Fig. 3a, b. J. C. Doyle coll. Figs 4a, b, 5. Coll. R. E. H. Reid. BM C79496, C79507, both × 2. See also Pl. 7, figs 10, 12.

Baculites undulatus d'Orbigny (p. 287). Reed.
Figs 6, 7, 8. J. C. Doyle coll. See also Pl. 7, fig. 11.

Allocrioceras angustum (J. de C. Sowerby) (p. 290). Hitch Wood.
Figs 9, 10. R. E. H. Reid coll. BM C79489, C79488. Fig. 11a, b. Specimen showing aperture. J. C. Doyle coll. 382.

Allocrioceras strangulatum sp. nov. (p. 291). Hitch Wood.
Figs 12, 14a, b. Paratypes, J. C. Doyle coll. 477, 352. Fig. 13a, b. **Holotype**, coll. R. E. H. Reid. BM C79490. See also Pl. 2, fig. 1.

Anisoceras reidi sp. nov. (above). Hitch Wood.
Fig. 15a, b. **Holotype**, coll. R. E. H. Reid. BM C79487. See Fig. 1, p. 290, for suture.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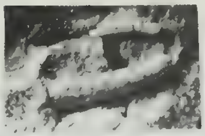
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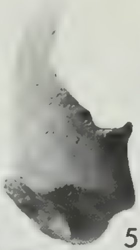
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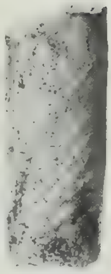
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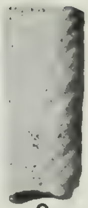
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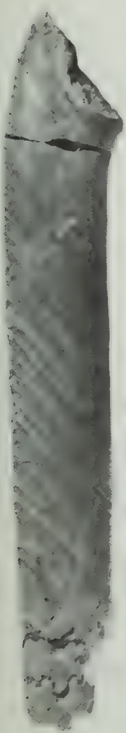
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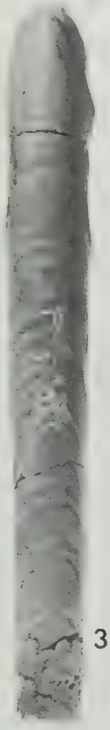
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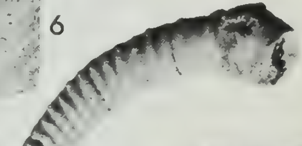
4a

4b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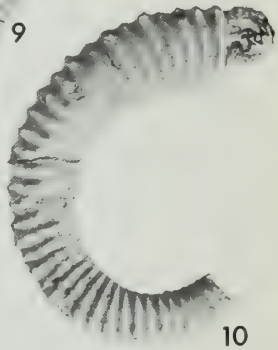
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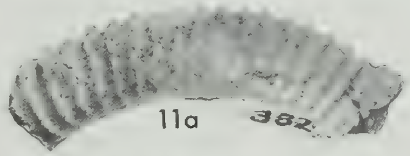
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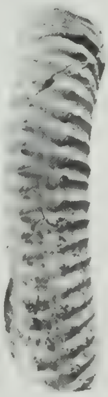
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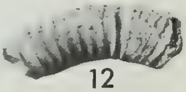
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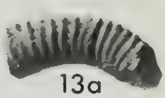
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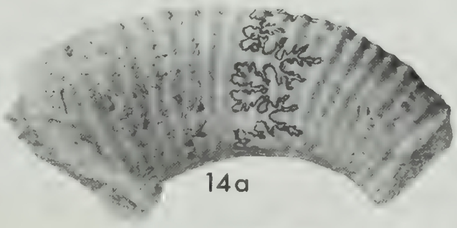
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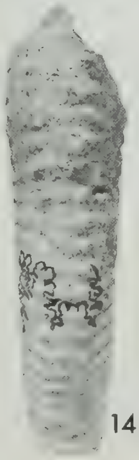
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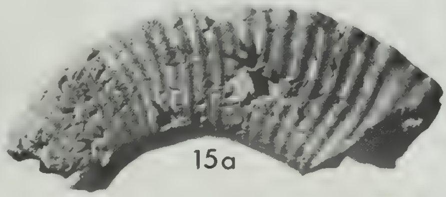
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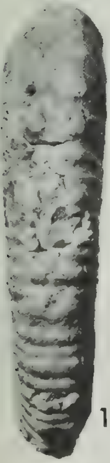
15b

old age. The main distinguishing features of *A. reidi* then are the doubling of the tuberculate ribs as they cross the venter and the length and narrowness of the second and third lateral saddles in the suture.

Of earlier species of *Anisoceras* the Upper Albian and Lower Cenomanian *A. campichei* Spath is perhaps closest to *A. reidi*, but it has sharper and more distant ribs which meet regularly in pairs at the ventrolateral tubercles.

OCCURRENCE. Only two undoubted specimens are known, from Hitch Wood and the Luton railway cutting.

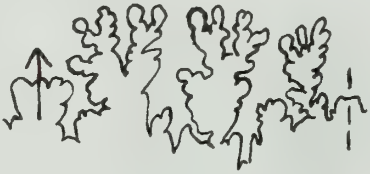

Fig. 1 Suture of *Anisoceras reidi* sp. nov., ×2.

Genus *ALLOCRIOCERAS* Spath, 1926

TYPE SPECIES. *Allocrioceras woodsi* Spath, 1926, = *Hamites angustus* J. de C. Sowerby, 1850.

Spath attributed this genus to his family Phlycticrioceratidae. The nominate genus of that family is with little doubt derived from *Allocrioceras* but differs from it and from most other hamitoid genera in having a siphonal row of tubercles. *Prophlycticrioceras* Clark from the Upper Albian of Texas seems to be an analogue rather than a direct ancestor. A little-known Coniacian genus *Boehmoceras* Riedel, 1931, doubtfully attributed to the same family, has an entire rounded keel and clearly does not belong here. Although *Allocrioceras* constitutes a fairly distinct group of species it does not have any characters of such importance as to justify its separation from the Anisoceratidae. Phlycticrioceratidae, if necessary as a taxon at all, are best regarded as a subfamily of Anisoceratidae and as including only the nominate genus.

Allocrioceras includes some species that are apparently regularly coiled in one plane and others that are rather irregular and generally rather helicoid, with the shell so twisted that the dorsoventral axis is at an angle greater than 90° to the axis of the spire. The ribs are normally single, regular or variable in strength, and in most species the majority carry ventrolateral tubercles. Constrictions may be present. The saddles of the suture are more or less regularly bifid. The lateral and umbilical lobes are asymmetric and not so obviously bifid as in some allied genera.

Allocrioceras is first known from the top of the Cenomanian in Britain and the U.S.A. (*A. annulatum* (Shumard). It may have been derived from *Idiohamites* of the group of *I. alternatus* (Mantell).

Allocrioceras angustum (J. de C. Sowerby)
Pl. 1, figs 9–11

1850 *Hamites angustus* J. de C. Sowerby, *in* Dixon : 346; pl. 29, fig. 12.
1850 *Hamites geinitzii* d'Orbigny : 215.
1876 *Crioceras ellipticum* Mantell sp.; Schlüter : 164; pl. 43, figs 1, 2 (*non* 1872 : 100; pl. 30, figs 11, 12).
1896 *Crioceras ellipticum* (Mantell); Woods : 84; pl. 3, figs 8–10.
1927 *Allocrioceras* aff. *ellipticum* (*non* Mantell) Woods sp.; Billinghurst : 517; pl. 16, fig. 4a–c.
1939 *Allocrioceras woodsi* Spath : 598.
1951 *Allocrioceras woodsi* Spath; Wright & Wright : 15.

DESCRIPTION. Coiled more or less regularly in a loose open spire, with the dorsoventral axis of the shell oblique to the axis of the spire. The body chamber levels out and uncoils, so that the last part may be almost straight. The section is oval, with a flat venter emphasized by the outwardly-directed ventrolateral spines present on all the ribs or on alternate ones. The ribs are alternately strong and weak and the tubercles on the weak ones, if present, are feebler than those on the strong ribs; the difference is sometimes marked (e.g. BM C33429). The ribs are fairly sharp and separated by distinctly wider interspaces; they may be radial, prorsiradiate or rursiradiate, varying with the coiling. The aperture has a flat striated margin, parallel with the ribs. The suture has moderately indented, squarish saddles, more or less symmetrically divided by lobules, and bifid lobes, the lateral and umbilical slightly asymmetrical. The first lateral saddle is the widest and the second lateral the narrowest of the three that are present.

AFFINITIES AND DIFFERENCES. *A. angustum* closely resembles its predecessor and presumed ancestor *A. annulatum* (Shumard). It differs in its less symmetrical and more irregular coiling, by its slightly irregular ribs, alternately strong and weak, by the feebleness or absence of tubercles on the weaker ribs and by the slightly to moderately compressed whorl section. No doubt in a series of specimens collected throughout the Turonian the variation in these characters would be found to be continuous, but *A. annulatum* is known in this country only from the uppermost Cenomanian with *Metoicoceras* and *Neocardioceras* and in the United States from that and slightly earlier horizons, whereas *A. angustum* occurs much later.

Woods (1896) recognized that Sowerby's *Hamites angustus* was the common Chalk Rock species but identified both, incorrectly, with Mantell's *Idiohamites ellipticus*, a Lower Cenomanian species with much more compressed section and more rounded ribbing. *Idiohamites alternatus* (Mantell), also Lower Cenomanian, is more distantly and coarsely ribbed and tuberculate. C. F. Römer (1870 : 322; pl. 37, fig. 10) figures as *Hamites ellipticus* a fragment with distant blunt ribs and apparently no tubercles; although he said that Dixon's *H. angustus* was 'probably synonymous', this seems unlikely.

OCCURRENCE. This is one of the commonest Chalk Rock species and is also known from the *Holaster planus* chalk in its nodular and normal facies, occurring even in Yorkshire.

Allocrioceras strangulatum sp. nov.

Pl. 1, figs 12–14; Pl. 2, fig. 1

1876 *Crioceras ellipticum* (Mantell); Schlüter : pl. 30, figs 11, 12 (*non* 1876 : pl. 43, figs 1, 2).

TYPES. The holotype is BM C79490 (WW coll.), the paratypes BM C79508 (WW coll.) and Doyle coll. 352 and 477, all from Hitch Wood.

NAME. 'Constricted.'

DESCRIPTION. Coiled in a moderately open, slightly helical spiral, perhaps irregular in the early stages. Section compressed oval. Constrictions are present but are sparse and rather feeble on the outer whorls. The ribs are rather fine and sinuous, almost biconcave, with paired ventral tubercles, rather close together on each rib; occasionally two ribs join at the ventrolateral tubercle. The ribs and tubercles are sharp on the early whorls but become blunter later, the tubercles then being slightly elongated spirally, instead of transversely as on the early part, and in some cases septispinate.

AFFINITIES AND DIFFERENCES. The compression, constrictions, sinuous ribs and the closeness of the ventral tubercles on the early whorls readily distinguish this species from *A. angustum* or *A. annulatum*. The English specimens compare well with Schlüter's *Crioceras ellipticum* (1876 : pl. 30, figs 11, 12) from the Turonian of Lengerich, in section, coiling, rib curve and tuberculation; despite the apparent absence of constrictions in the German specimen it is presumably the same species.

OCCURRENCE. In England it is known only from Hitch Wood and Kensworth, where it is rare. It occurs also in Germany.

Allocrioceras billinghursti Klinger

Pl. 2, figs 2, 3a, b

1874 *Helicoceras ellipticum* (Mantell); Geinitz : 194; pl. 35, figs 14–16.
1927 *Allocrioceras* sp. ind. Billinghurst : 617; pl. 16, fig. 7a, b.
1976 *Allocrioceras billinghursti* (Wright MS) Klinger : 32; pl. 9, fig. 2a, b; text-fig. 7b.

TYPES. Klinger merely designated as holotype 'Geinitz pl. 35, fig. 16'. The originals of Geinitz' figs 14 and 15 and of Billinghurst's pl. 16, fig. 7a, b (BM C32298), which were cited in Klinger's synonymy, as well as the latter's Zululand specimens GSP Z1598 and Z2069, are paratypes.

MATERIAL. The following English specimens were cited in drafts of the present paper from which Klinger presumably took the specific name: BM C78510, C79650–2 (WW *ex* Reid coll.), BM C79505–6 (WW *ex* Bromley coll.), all from Hitch Wood; A. Wainwright coll. J62 from Kensworth and R. Bromley coll. C158 from Reed.

DESCRIPTION. Coiled in an open, apparently more or less regular helical spire; markedly torticone, with the long diameter of the whorl section oblique to the axis of the spire. The ribs are almost vertical if fragments are placed so that the axis of the spire would be vertical. They are strong and well spaced, fairly sharp at first but becoming more rounded later. The main ribs bear rather strong spines, which on later parts of the shell become septate so that only flat spine bases are seen on internal moulds. Between the main ribs there are one or two that are weaker on the venter; in the early stages such ribs carry spines but later they are untuberculate. The suture is florid at later growth stages but still has the wide, more or less parallel-sided and equal saddles typical of *Allocrioceras*.

AFFINITIES AND DIFFERENCES. The stronger ribs in the early stages and the more helical and strongly torticone coiling serve to distinguish this species from contemporary members of the genus. Some specimens of the uppermost Cenomanian and basal Turonian *A. annulatum* (Shumard) approach the present species in these respects but are not so torticone and have much weaker ventrolateral spines. A few specimens of *A. billinghursti* (e.g. BM C33430) have rather finer, closer and more regular ribs than the typical form and thus are closer to *A. angustum*. Large fragments like BM C79510 and Geinitz' specimens resemble many nostoceratids in the swung ribs and coiling, but the suture remains typical of *Allocrioceras* and has no resemblance to the nostoceratid type with deeply dissected, overhanging and narrow-based first lateral saddle.

OCCURRENCE. In England in the Chalk Rock of Hitch Wood, Kensworth and Reed; in the Turonian of Saxony and in the Lower Coniacian of Zululand.

Allocrioceras (?) cf. *cuvieri* (Schlüter)

cf. 1872 *Ancyloceras cuvieri* Schlüter : 97; pl. 30, figs 3, 4.

DESCRIPTION. A single specimen in J. C. Doyle's collection, comprising two fragments of compressed, more or less criocone early whorls with maximum whorl height of 11 mm and breadth of 8·5 mm, seems to compare best with Schlüter's species, founded on a specimen from the 'Cuvieri-Pläner' of Salzgitter. The English specimen has regular prorsiradiate rounded ribs, six in a distance corresponding to the larger diameter, with slight but distinct bullate ventrolateral tubercles; the ribs at first are interrupted on the venter but later cross it transversely, while the tubercles weaken. An enlarged rounded rib is visible at the anterior end of the larger fragment.

AFFINITIES AND DIFFERENCES. The German holotype is at its smaller end nearly twice the diameter of the English specimen and exact comparison is therefore impossible. It has prominent ventrolateral tubercles on the periodic enlarged ribs but it is not clear whether there were also tubercles on the minor ribs. The English specimen somewhat resembles *Allocrioceras strangulatum* sp. nov. (p. 291) in peripheral view but the prorsiradiate ribs, rounded from an early stage of growth, readily distinguish it.

The periodic enlarged ribs are unlike anything seen in other species of *Allocrioceras* but the present form is probably best placed in this genus.

OCCURRENCE. Chalk Rock of Kensworth.

Genus *NEOCRIOCERAS* Spath, 1921

This genus was based on an unidentified form allied to, but according to Shimizu (1933 : 15) distinct from, *Crioceras spinigerum* Jimbo, 1894, but that species was subsequently designated as type by Diener (1925 : 192). This is an apparently criocone form, perhaps with initial whorls not in one plane, with fine close ribs on some of which there are midlateral and on others ventrolateral tubercles, the latter alternating on the venter. Other species with more or less straight shafts, that had from time to time been referred to *Neocrioceras*, were rightly separated from the typical species as a distinct subgenus *Schlueterella* Wiedmann (1962 : 205) with type species *Ancyloceras pseudoarmatum* Schlüter, 1872; Wiedmann doubted indeed whether the two subgenera were of the same phylogenetic origin. Subsequently Collignon (1969 : 47) described a new genus *Christophoceras*, with a type species based on a magnificent body chamber with straight shaft and final hook, that is undoubtedly a synonym of *N.* (*Schlueterella*). The form described below is very similar to Collignon's.

Subgenus *SCHLUETERELLA* Wiedmann, 1962

Neocrioceras (*Schlueterella*) *multinodosum* (Schlüter)

Pl. 2, figs 4, 5

1872 *Hamites multinodosus* Schlüter : 106; pl. 32, figs 1, 2.

DESCRIPTION. The English material comprises a small but uncrushed specimen (GSM 108903), apparently at the stage where the shell has just straightened after a bend, and a very small fragment of a slightly larger specimen (Doyle coll. 469). The section is oval. There are periodic rectiradiate ribs which bear prominent spines high up on the sides, joined by looped riblets to prominent paired ventral spines, similarly joined across the venter by looped riblets. Between these major ribs there are slightly less strong ones, seven in number in this small fragment, with small but distinct ventrolateral and ventral spines similar in position to those on the major ribs.

AFFINITIES AND DIFFERENCES. The English specimen figured in Pl. 2, fig. 5 is at about the same growth stage as the holotype of *Neocrioceras* (*S*). *sanushibense* Wright & Matsumoto (1954 : 121; pl. 7, fig. 5a, b) from the Upper Santonian of Japan, but differs in having a more compressed section and seven as opposed to three or four intermediate minor ribs, which moreover do not tend to join at the ventrolateral tubercles. All the characters suggest the association of the English specimens with Schlüter's crushed and fragmentary holotype of *H. multinodosus*; at a considerably later growth stage than the English material this has five minor ribs between the major ones; taking into account the Campanian *N.* (*S.*) *pseudoarmatum* (Schlüter) which has only one or two intermediate ribs (Schlüter 1872 : 99; pl. 31, figs 1–3; 1876 : pl. 43, figs 5–9) one would expect the number to decrease from early to later stages in phylogeny.

The periodic enlarged ribs with looped riblets between the tubercles on shoulder and venter distinguish *Neocrioceras* from most species of the otherwise rather similar *Pseudoxybeloceras*. However, *Ancyloceras lineatum* Gabb and *Oxybeloceras petrolense* Anderson, referred by Matsumoto (1959 : 162) to *Pseudoxybeloceras*, have occasional major ribs of *Neocrioceras* type. Indeed the present form is particularly interesting in that its abundant straight minor ribs strongly recall the ribs of *Pseudoxybeloceras* (cf. Wright & Matsumoto 1954: text-figs 9–12). The two genera are now both known to range from Upper Turonian to Campanian and one is probably derived from the other. If the decrease in the number of minor ribs between each pair of major ones from seven in the Turonian *N. multinodosum* to three or four in the Santonian *N. sanushibense* and one or two in the Campanian *N. pseudoarmatum* is taken to indicate that the enlarged major ribs were a new feature when the genus first arose, then *Neocrioceras* was derived from *Pseudoxybeloceras* rather than the reverse.

OCCURRENCE. Single fragments each from Reed, Hitch Wood and north Germany.

Family **TURRILITIDAE** Meek, 1876

Subfamily **NOSTOCERATINAE** Hyatt, 1894

Howarth (1965 : 371–374) has reviewed the classification of this family and in particular Wiedmann's (1962) drastic reduction of the three most widely used genera to the status of synonyms of *Cirroceras* Conrad, 1868. I agree with Howarth that *Cirroceras*, which I accepted as senior synonym of *Didymoceras* Hyatt, 1894 (Wright 1957*b*), should be treated as a *nomen dubium*, and I also accept his conclusion that *Bostrychoceras* and *Didymoceras* are best regarded as synonymous.

Genus ***DIDYMOCERAS*** Hyatt, 1894

TYPE SPECIES. *D. nebraskense* Hyatt.

Didymoceras (including *Bostrychoceras* Hyatt, see Howarth 1965) was long regarded as an Upper Senonian genus; earlier species with similar coiling and ribbing were referred, by Billinghurst (1927 : 513) for example, to *Hyphantoceras*, whose type species has very irregular coiling and different ornament. In fact there is a series of species beginning with *D. thomasi* (Pervinquière) from the Upper Cenomanian of Algeria and continuing to the Campanian forms with whorls regularly in contact until the body chamber, which become increasingly U-shaped, and have regular dense ribbing. The main differences between species lie in the apical angle, the numbers, angle and curve of the ribs and the numbers and form of constrictions. These early *Didymoceras* differ little from Middle Albian *Proturrilitoides*, from survivors of which they were presumably derived, except in the pendent, incipiently U-shaped body chamber. By the Campanian, however,

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Plate 2 ×1

Allocrioceras strangulatum sp. nov. (p. 291). Hitch Wood.
Fig. 1. Closely-ribbed specimen with occasional looped ribs. Paratype, J. C. Doyle coll. 358. See also Pl. 1, figs 12–14.

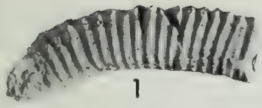
Allocrioceras billinghursti Klinger (p. 292). Hitch Wood.
Fig. 2. The species is always twisted so that both right and left ventrolateral tubercles are visible in this view. Coll. WW. BM C79510. Fig. 3. Later whorls with blunt ribs, coll. R. G. Bromley. BM C79505.

Neocrioceras (*Schlueterella*) *multinodosum* (Schlüter) (p. 293).
Fig. 4. Hitch Wood. Doubtful fragment. J. C. Doyle coll. 469. Fig. 5a, b. Reed. Body-chamber fragment, coll. C. J. Wood. GSM 108903.

Hyphantoceras reussianum (d'Orbigny) (p. 297). Hitch Wood.
Fig. 6. End of camerate part and regular pendent body chamber, J. C. Doyle coll. 1288. Fig. 7. Irregular body chamber with expanded aperture, coll. WW. BM C79478. See also Pl. 7, figs 4, 6.

Didymoceras saxonicum (Schlüter) (p. 296).
Figs 8, 9a, b. Hitch Wood. Fig. 8 shows reversal of direction of ribs between the first and second preserved whorls. Coll. R. E. H. Reid. BM C79491, C79492. Fig. 10. Hitch Wood. Body chamber of sinistral individual. Coll. WW. BM C79476. Fig. 11. Hitch Wood. Body chamber of dextral individual showing penultimate and ultimate constrictions. J. C. Doyle coll. 647. Fig. 12. Cuckhamsley Knob. Specimen with unusually fine ribs. SM B4253. See also Pl. 7, fig. 5.

Photograph: Fig. 2 by BM.



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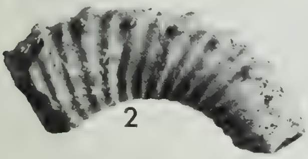

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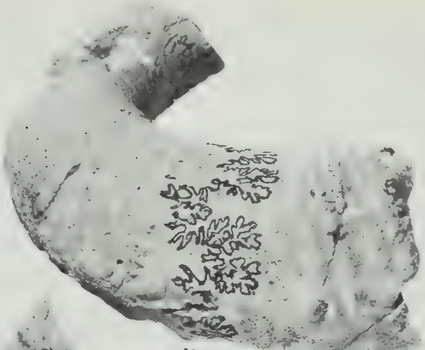

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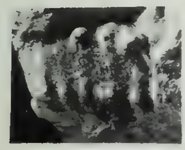

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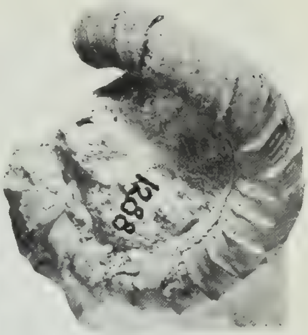

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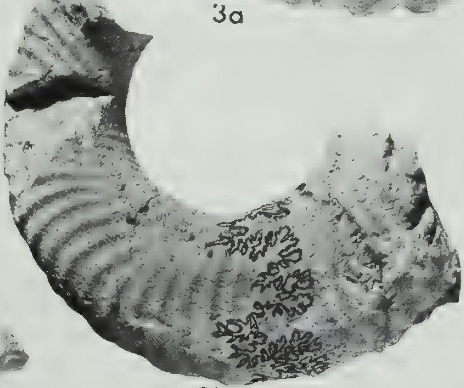

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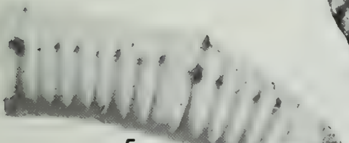

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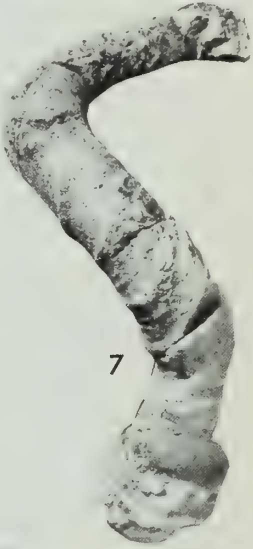

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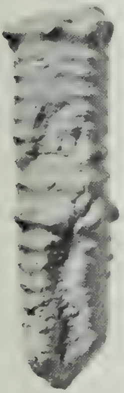

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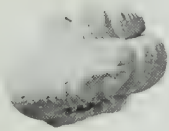

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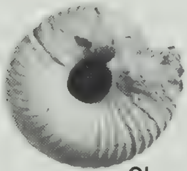

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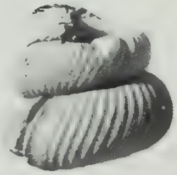

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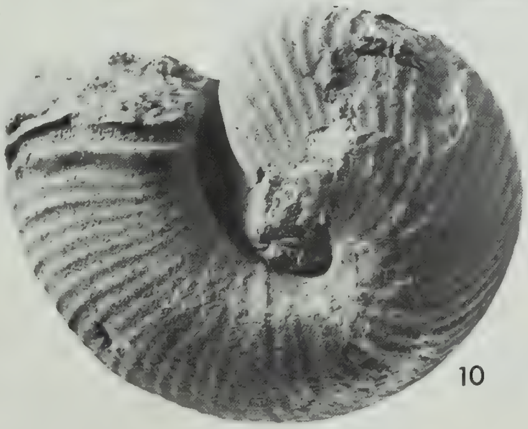

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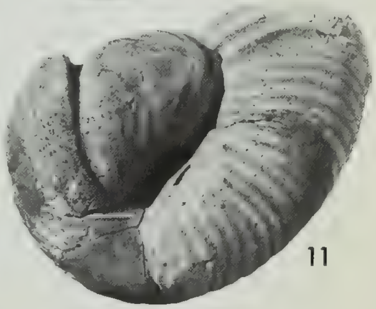

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12

additional forms appear in which the last few whorls before the body chamber become uncoiled and may be more or less regularly bituberculate. These include the type species of the genus; among such species probably lies the origin of *Nostoceras* with regular bituberculate ribbing (Howarth 1965 : 372–374). *Eubostrychoceras* Matsumoto (1967 : 332), created for the pre-Campanian species, I would now regard as unnecessary, but it might reasonably be employed as a subgenus.

Didymoceras saxonicum (Schlüter)

Pl. 2, figs 8–12; Pl. 7, fig. 5

1840 *Turrilites undulatus* Mantell; Geinitz : 42; pl. 13, fig. 1 only.
1841 *Turrilites polyplocus* F. A. Römer : pl. 14, fig. 2 only.
1843 *Turrilites polyplocus* Römer; Geinitz: 67; pl. 13, fig. 1.
1846 *Turrilites polyplocus* Römer; Geinitz : pl. 12, fig. 3.
1850 *Turrilites Geinitzii* d'Orbigny : 216.
1870 *Turrilites polyplocus* F. A. Römer; C. F. Römer : 321; pl. 36, fig. 1.
1872 *Turrilites Geinitzii* d'Orbigny; Schlüter : 113; pl. 35, fig. 10.
1874 *Turrilites polyplocus* F. A. Römer; Geinitz : 195; pl. 36, figs 1–3.
1875 *Turrilites saxonicus* Schlüter : 30.
1876 *Turrilites saxonicus* Schlüter; Schlüter : 135.
1895 *Turrilites saxonicus* Schlüter; Kossmat : 143.
1896 *Heteroceras* sp. Woods : 75; pl. 2, figs 6–8.
1922 *Heteroceras woodsi* Kitchin : 49.
1927 *Hyphantoceras woodsi* (Kitchin) Billinghurst : 517; pl. 16, figs 5, 6.
1962 *Cirroceras (Cirroceras) indicum saxonicum* (Schlüter) Wiedmann : 203.

Description. Coiled in a sinistral or dextral spire with a wide umbilicus and with the whorls in contact until the slightly pendent U-shaped body chamber. The whorl section in the early stages is round, subquadrate or slightly oval but becomes increasingly oval with age. There are two or three oblique constrictions to a whorl; on the internal mould they are rather deep with rounded edges but on the shell they have sharp collars. On the later whorls they are strongly undercut and towards the end the front collar is directed backwards over the constriction. The shell increases suddenly in cross section after each constriction. Between constrictions there are fine, regular, sharp or rounded, single or branching ribs, separated by slightly wider interspaces. The density of ribbing varies between individuals but there are normally about 90 ribs to a whorl, many branched low on the side. The ribs and constrictions are always oblique and on most of the shell are directed forwards from the upper margin, but in some individuals they are directed backwards for a few whorls and then change direction (Pl. 2, fig. 8). On the more oval later whorls the ribs are very sinuous. The pendent body chamber turns up at the end and has a final constriction with sharp collars. The siphuncle is in the middle of the outer side of the whorl. The suture has rather florid bifid elements; the first lateral lobe is the widest and undercuts the first lateral (external) saddle, reaching almost to the siphuncle on one side and the umbilical lobe on the other. A small fragment of the early stages (BM C79470) from the *Holaster planus* Zone of the Guildford bypass indicates a shell with a right-angled bend in one plane followed by three more or less straight shafts, up to 9 mm long, joined by right-angled bends in another plane. This fragment links with the specimen figured in Pl .7, fig. 5 and suggests that the species had irregular and possibly heterostrophic early whorls. To the best of my knowledge no normally-coiled initial whorls of the species have been found.

Affinities and differences. The much later (Campanian) *D. polyplocum* has more inflated whorls than *D. saxonicum*, no constrictions, straighter ribs, a freer pendent body chamber and no sudden change in whorl section at the end of the spire. The Coniacian *D. indicum* (Stoliczka) appears to have distinctly less oblique and stronger ribs and a more acute apical angle than *D. saxonicum*, with a consequential narrower umbilicus. Kossmat (1895 : 143) recognized the close similarity of the two forms and it may be that *D. saxonicum* should be treated as a subspecies of *indicum*. Indeed Wiedmann (1962 : 202) treated these two, with *elongatum* of Whiteaves, as subspecies of a variable long-ranging species. I am not yet satisfied that this is justified and prefer to maintain the three as distinct species for the present.

NOMENCLATURE. Geinitz' (1839) specimen of '*Turrilites undulatus*' was referred by Römer (1841) to his species *polyplocus*, but since Geinitz described it from areas, such as Strehlen, noted for their Turonian faunas it presumably belongs to the present species. D'Orbigny's (1850 : 216) species *geinitzii* was based only on one of Geinitz' specimens (1840 : pl. 13, fig. 3); later Geinitz (1874 : 195) stated that this specimen was too badly preserved for specific determination, an opinion which the illustration supports. Schlüter (1872 : pl. 35, fig. 10) figured a specimen as *T. geinitzii* d'Orbigny, but Geinitz in 1874 said that this was not the same species as d'Orbigny's *T. geinitzii*, based on Geinitz' own badly-preserved example. In the light of his statement the name cannot be regarded as validated by Schlüter's description of good and identifiable material, as might otherwise have been the case. *T. geinitzii* must therefore be treated as a *nomen dubium*, being based only on unidentifiable material. Schlüter recognized this and (1875 : 30) named the species *Turrilites saxonicus*, represented in his figure of 1872 (pl. 35, fig. 10). He used the same name in a later part of his monograph (Schlüter 1876 : 135), where he gave a synonymy that largely agrees with that given above, but under '1841 *Turrilites polyplocus* Ad. Römer' he cited 'pl. 14, fig. 1 (non! fig. 2).' This is the reverse of what would accord with the rest of his synonymy and is presumably a mistake.

OCCURRENCE. Abundant in Hertfordshire, Bedfordshire and Buckinghamshire but rare elsewhere in England. It occurs also in north and south Germany and in Czechoslovakia.

Genus *HYPHANTOCERAS* Hyatt, 1900

TYPE SPECIES. *Hamites reussianus* d'Orbigny, 1850.

Shorn of the species now referred to *Didymoceras*, *Hyphantoceras* is a well-circumscribed genus, characterized by loose and frequently irregular coiling in three dimensions, distant main ribs, thin and high with two to four flare-like tubercles, with or without fine feeble intermediate ribs. The suture is florid and similar to that of *Didymoceras*.

H. reussianum is the earliest known species. It could well have been derived from some early species of *Didymoceras* by loosening of the coiling, loss of the constrictions and development of flared main ribs perhaps from the collars of *Didymoceras*. Later species differing in coiling and details of the ribbing range into the Santonian.

Hyphantoceras reussianum (d'Orbigny)

Pl. 2, figs 6, 7; Pl. 7, figs 4, 6

1840 *Hamites plicatilis* Mantell; Geinitz : 41; pl. 12, fig. 4; pl. 14, fig. 2.
1841 *Hamites plicatilis* Sowerby; F. A. Römer : 94; pl. 14, fig. 7.
1843 *Hamites plicatilis* Sowerby; Geinitz : 8; pl. 5, fig. 2.
1843 *Turrilites polyplocus* var. Geinitz : 8; pl. 5, fig. 4.
1845 *Hamites plicatilis* Sowerby; Reuss : 23; pl. 7, figs 5, 6.
? 1845 *Turrilites Astierianus* d'Orbigny; Reuss: 24; pl. 7, fig. 7.
1846 *Hamites armatus* d'Orbigny; Geinitz : 304; pl. 12, fig. 3.
1850 *Hamites reussianus* d'Orbigny : 216.
1861 *Anisoceras Reussianus* (d'Orbigny) Pictet & Campiche : 76.
1870 *Helicoceras annulifer* C. F. Römer : 320; pl. 36, fig. 2.
1872 *Heteroceras Reussianum* (d'Orbigny) Schlüter : 109; pl. 32, figs 13–21; pl. 33, fig. 1.
1872 *Helicoceras armatus* d'Orbigny; Fritsch : 47; pl. 13, fig. 16; pl. 14, figs 8, 17 only.
1874 *Helicoceras Reussianum* d'Orbigny; Geinitz : 193, pl. 35, figs 11, 12.
1889 *Helicoceras Reussianum* Geinitz; Fritsch : 71, text-fig. 44.
1896 *Heteroceras Reussianum* (d'Orbigny); Woods : 74; pl. 2, figs 3–5.
1900 *Hyphantoceras Roissyanum* (Schlüter); Hyatt : 587.
1910 *Heteroceras reussianum* (d'Orbigny); Crick : 347; pl. 27, fig. 3.

1913 *Hamites* sp.; Roman & Mazeran : 19; pl. 4, fig. 19.
1951 *Hyphantoceras reussianum* (d'Orbigny); Wright & Wright : 18.
? 1957*a* *Hyphantoceras* cf. *reussianum* (d'Orbigny); Wright : 806; pl. 54, fig. 2a, b.

DESCRIPTION. More or less irregularly coiled; some specimens consist of a fairly regular open or tightly coiled conical helix, with a pendent U-shaped body chamber (Pl. 2, fig. 6); occasionally the helix is cylindrical (Schlüter 1872: pl. 32, fig. 18); in other cases the coiling is very irregular, especially in the later stages (Pl. 2, fig. 7). The cross section increases very slowly. The early stages of *H. reussianum* are similar (BM C79471 from Sparsholt, Berkshire) to the heterostrophic initial whorls of *H. reflexum* (Quenstedt) that have been figured (Fritsch 1872 : pl. 14, figs 14–16, 18). The major ribs at most growth stages are thin, high and distant on the body chamber and normally carry four fairly distinct tubercles, but at earlier stages they may have four, two or no tubercles. Between them is a variable number of ribs or striae. The suture is very similar to that of *D. saxonicum*.

AFFINITIES AND DIFFERENCES. On the early whorls the major ribs may be closer than on the later but even on whorls only 2 mm high (BM C79471) there are two or three intermediaries, a feature which clearly distinguishes the species from *H. reflexum*, as Schlüter eventually (1876 : 166) concluded. *H. flexuosum* (Schlüter), which is of slightly later date than *H. reussianum*, differs in having less differentiated major and minor ribs and, apparently, no tubercles. Some loosely coiled specimens (e.g. Pl. 7, fig. 4), show no major ribs, at least on internal moulds, on considerable lengths of shell. These are probably fragments of aberrant specimens of the present species.

OCCURRENCE. *H. reussianum* is widespread in England and occurs both in the Chalk Rock and nodular facies and also occasionally in the normal *Holaster planus* Zone chalk of Lincolnshire and Yorkshire, from which several large U-shaped body chamber fragments have come. Abroad it is widely distributed in northern and central Europe and a probable example is recorded from New Zealand (Wright 1957 : 806; pl. 54, fig. 2a, b).

Family **SCAPHITIDAE** Meek, 1876

The family apparently originates early in the Upper Albian and by the Cenomanian a variety of species of two groups, one involute and without lappets (Scaphitinae), the other evolute and with lappets (Otoscaphitinae), is widespread in most parts of the world. The case for maintaining these as subfamilies (Wright 1953) despite Wiedmann's objections (1965) is being made in a separate paper. Only a very few species, however, seem to survive the end of the Cenomanian and it is not until the latter part of the Turonian that either stock becomes abundant again. The Scaphitinae begin at this time to radiate and during the Coniacian and Santonian there is great expansion in the number of species. The particular interest of the late Turonian forms described below is that they are beginning to foreshadow some of this expansion; the origins of several Coniacian species can be clearly seen among variants of the *Scaphites geinitzii* group.

Subfamily **SCAPHITINAE** Meek, 1876

Several species and subspecies are distinguished below among the Chalk Rock fauna, but they are all closely related and a case could be made for treating most of them as variants of *Scaphites geinitzii*.

Genus ***SCAPHITES*** Parkinson, 1811

TYPE SPECIES. *S. equalis* J. Sowerby, 1813.

Scaphites geinitzii d'Orbigny

(For synonymy see under the subspecies.)

DESCRIPTION. The size varies from about 20 to about 60 mm in greatest length and the maximum thickness ranges from about 35% to about 50% of the length. The density of ribbing is also variable. On the spire the ribs are normally slightly sinuous and the primaries split half to two-thirds of the way up the side into two to four secondaries. On the shaft and hook the primaries give rise to three to five secondaries. On the later part of the shaft and on the hook the point of branching is raised into a more or less distinct tubercle which varies from a feeble bulla in the compressed forms to a prominent one in inflated specimens. Normally these tubercles number between six and nine and there are no distinct umbilical ones. Inflated and compressed forms are equally involute; the beginning of the shaft conceals up to half or even more of the small umbilicus. The suture is relatively simple with rather regularly bifid lateral saddles and lobes.

REMARKS. The name *Scaphites geinitzii* was first published by d'Orbigny in the Prodrome (**2**, 1850 : 214) as follows:

> * 58. *Geinitzii*, d'Orb., 1847. Espèce voisine du *Scaphites obliquus*, mais pourvue de plis tuberculeux externes. *Scaph. aequalis*, Geinitz (non Sowerby). France, Villedieu (Loire-et-Cher); Dresde, Strehlen.

The asterisk indicates that d'Orbigny had specimens in his own collection. Monsieur J. Sornay has with great kindness sent me plaster casts of three specimens, labelled as from Strehlen, in the d'Orbigny collection, which he reports contains no *Scaphites* from Villedieu.

Opinion 126 of the International Commission on Zoological Nomenclature ('Opinions and Declarations' **1**, Sec. B, Facsimile Edition, London, 1958) lays down that the 'Prodrome' should be regarded as containing preliminary diagnoses and that the adequacy of the diagnosis is for the systematist to assess in each case. The diagnosis of *Scaphites geinitzii* differentiates the species from two earlier ones and refers to the characteristic outer tubercles. The name is certainly in common use for the abundant and widespread tuberculated Upper Turonian *Scaphites* of Europe. It seems reasonable to hold that the words of the description coupled with the mention of Strehlen and the survival in the d'Orbigny collection of Strehlen specimens amount to an adequate diagnosis.

Of d'Orbigny's three specimens, all more or less crushed, two clearly belong to the species generally known as *Scaphites geinitzii*. The third is either a different species, resembling Yabe's *Yezoites planus* (1910 : 167; pl. 18, fig. 14), or, more probably, a pathological specimen of *S. geinitzii*. I designate as **lectotype** a complete but distorted specimen, one of two numbered 7197, of which a plaster cast is here figured (Pl. 3, fig. 1).

A further nomenclatorial complication arises from the fact that Römer described (1841 : 86; pl. 13, fig. 4) as *Ammonites cottae* a specimen that, despite Wiedmann's (1965 : 430) reference to it as *S.* (*Otoscaphites*) *cottae* (Römer), seems to me to be the spire of *S. geinitzii*. This conclusion has been reached by most subsequent authors, but none has taken the consequential step of reviving Römer's name in preference to *geinitzii*. In order to stabilize accepted usage an application to conserve the name *geinitzii* will be made to the International Commission on Zoological Nomenclature.

It is important to ascertain where the type lies in the rather wide range of forms included in *S. geinitzii*. The specimen figured in Pl. 3, fig. 2 closely resembles the lectotype in whorl section, rib density and form of tubercles. It may safely be regarded as typical of the species. This specimen is the original of Woods (1896: pl. 3, fig. 6).

Examination of the figures in the literature and of a fairly large number of specimens from the English Chalk Rock suggest that this variable species should be widely drawn. The stock seems to include in the Upper Turonian a range of forms differing in degree of inflation, density of ribbing and strength of ribs and tubercles. By the beginning of the Coniacian the variation is discontinuous and a number of good species can be separated. These are foreshadowed in the Upper Turonian material but most of it cannot be separated into distinct species. Subspecies however can be usefully distinguished in some cases and a limited number are established below. In all of these subspecies the degree of involution, the general pattern of ribs and tubercles and the direction of the ribbing on the shaft remain noticeably constant.

Apart from the subspecies here described there occurs in Germany (e.g. Schlüter 1872 : pl. 23, figs 2, 13) and Czechoslovakia an inflated form in which the ventrolateral tubercles become increasingly prominent and clavate. This is probably a slightly later offshoot of *S. g. intermedius* Scupin and leads directly to the Lower Coniacian *S. meslei* Grossouvre, which, *pace* Sturm (1901 : 61), followed by Scupin (1913 : 101), is not the same as *S. kieslingwaldensis* Langenham & Grundey (see p. 303).

OCCURRENCE. *S. geinitzii* is recorded from the Zone of *Terebratulina lata* in this country, probably therefore from the horizon of *Collignoniceras woollgari* (as in Germany – Schlüter 1876 : 221) but good specimens are not known. It is abundant in the Zone of *Holaster planus*. It also ranges in England into the Zone of *Micraster cortestudinarium* (lower Coniacian) and in France (Aude) into the middle Coniacian. The occurrences in Saxony and Czechoslovakia were reviewed in an important paper by Prescher (1963).

Scaphites geinitzii geinitzii d'Orbigny

Pl. 3, figs 1–4, 6–7; Pl. 7, fig. 9

1840 *Scaphites aequalis* Sowerby; Geinitz : 40.
1841 *Scaphites costatus* Mantell; F. A. Römer : 90.
1841 *Ammonites Cottae* F. A. Römer : 86; pl. 13, fig. 4.
1850 *Scaphites Geinitzii* d'Orbigny : 214.

Plate 3 ×1

Scaphites geinitzii d'Orbigny (above).
Fig. 1. Upper Turonian, Strehlen, Saxony. Plaster cast of crushed **lectotype**. Musée d'Histoire Naturelle, Paris, 7197; d'Orbigny coll. Figs 2, 6, 7. Chalk Rock, Cuckhamsley Knob. Fig. 2 original of Woods 1896: pl. 3, fig. 6, 6a. Coll. Montague Smith. SM B4206, B4221, B4215. Fig. 3a, b. Hitch Wood. Coll. C. J. Wood. GSM 108884. Fig. 4. Hitch Wood. Coll. WW. BM C79475. See also Pl. 7, fig. 9.

Scaphites pseudoaequalis Yabe (p. 305). Cuckhamsley Knob.
Fig. 5. Original of Woods 1896: pl. 3, fig. 5, 5a. Coll. Montague Smith. SM B4205. See also Pl. 7, fig. 1.

Scaphites geinitzii laevior subsp. nov. (p. 302).
Fig. 8. Reed. **Holotype**, SM B594. Fig. 9. Cuckhamsley Knob. Paratype, coll. Montague Smith. SM B4208. See also Pl. 7, fig. 7.

Scaphites kieslingwaldensis Langenhan & Grundey (p. 303).
Fig. 10. Cuckhamsley Knob. Coll. Montague Smith. SM B4212. Figs 11a, b, 12a, b. Hitch Wood. Coll. R. E. H. Reid. Fig. 11, broad-ventered form retaining the sinuous ribs of *S. geinitzii* on the spire. BM C79579. Fig. 12, form with weak tubercles on the hook. BM C79485.

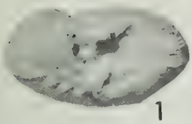
Scaphites lamberti doylei subsp. nov. (p. 304). Hitch Wood.
Fig. 13. **Holotype**, coll. R. E. H. Reid. BM C79486.

Scaphites diana sp. nov. (p. 304).
Fig. 14a, b. Hitch Wood. Paratype, coll. R. E. H. Reid. BM C79515. Fig. 15. Cuckhamsley Knob. **Holotype**, coll. Montague Smith. SM B21299. Fig. 16a, b. Hitch Wood, Paratype, J. C. Doyle coll. 645.

Otoscaphites reidi sp. nov. (p. 307).
Fig. 17. Medmenham. Paratype, coll. R. E. H. Reid. BM C79498. Fig. 18. Hitch Wood. Paratype, coll. WW. BM C79511. See also Pl. 7, fig. 8.

Otoscaphites bladenensis (Schlüter) (p. 305). *Holaster planus* Zone.
Fig. 19. Mickleham bypass. Original of Wright & Wright 1945: pl. 5, fig. 1a–c (as *Scaphites auritus*). Coll. WW. BM C79517. Fig. 20. Guildford bypass. Original of Wright & Wright 1945: pl. 5, fig. 2a, b (as *S. auritus*). Coll. WW. BM C79518.

Lewesiceras woodi sp. nov. (p. 312). Hitch Wood.
Fig. 21a, b. **Holotype**, coll. R. E. H. Reid. BM C79509. See also Pl. 6, fig. 6.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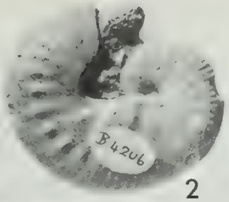

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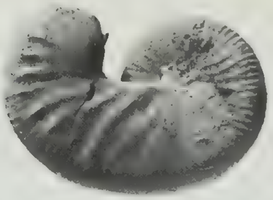
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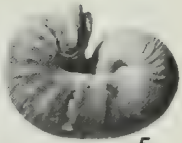
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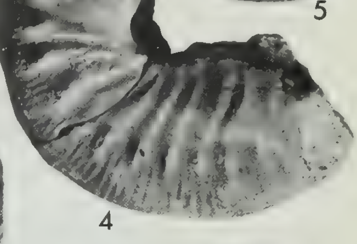
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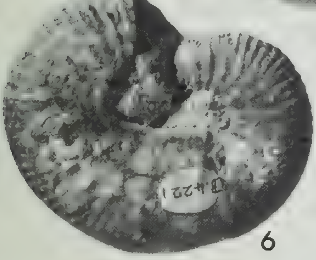

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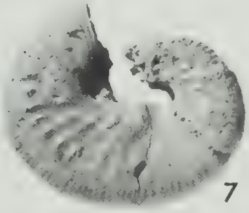
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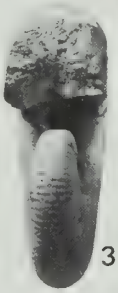
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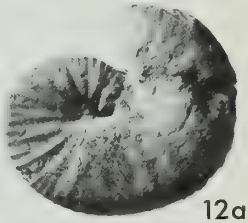
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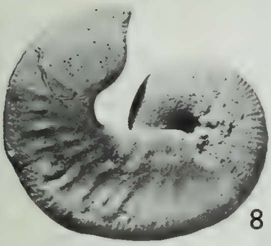
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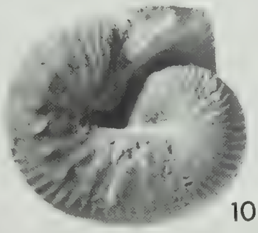
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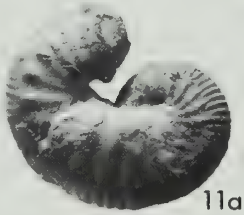
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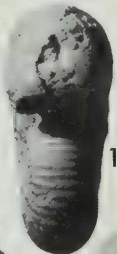
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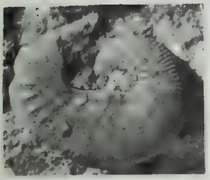
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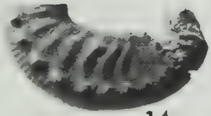
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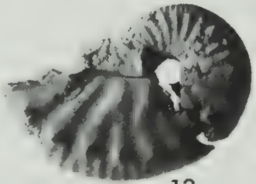
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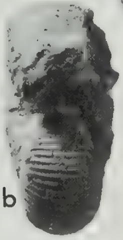
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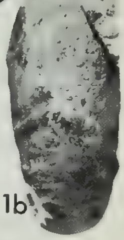
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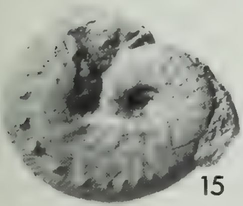
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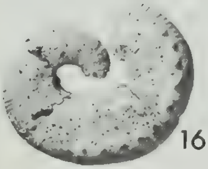
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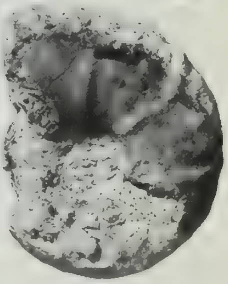
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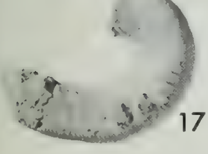
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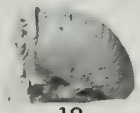
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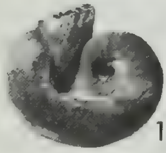
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1855 *Ammonites wiltonensis* Sharpe : 53; pl. 23, fig. 10.
1870 *Scaphites Geinitzii* d'Orbigny; C. F. Römer : 320; pl. 35, fig. 6.
1872 *Scaphites Geinitzii* d'Orbigny; Schlüter : 75; pl. 23, figs 14–16 only.
1872 *Scaphites Geinitzii* d'Orbigny; Fritsch : 42; pl. 13, fig. 12a–c only.
1874 *Scaphites geinitzi* d'Orbigny; Geinitz: 191; pl. 35, figs 1–4.
1889 *Scaphites geinitzi* d'Orbigny; Fritsch : 71, fig. 43.
1895 Übergangsform zwischen *Scaphites* cf. *Geinitzi* var. *Lamberti* Grossouvre und *Scaphites Geinitzi* d'Orbigny; Jahn : 138; pl. 8, fig. 2a–d.
1896 *Scaphites Geinitzi* d'Orbigny; Woods : 81; pl. 3, figs 6, 7 only.

DESCRIPTION. Compressed to moderately inflated. The ribs are rather coarse and slightly sinuous on the spire. On the shaft the primaries are broad and flat, branching at prominent pointed ventrolateral tubercles into three or four rather distant fine secondaries. On the hook the primary ribs are less flattened.

Scaphites geinitzii intermedius Scupin

1872 *Scaphites Geinitzii* var. *binodosus* Römer; Fritsch : 42; pl. 14, fig. 13a, b.
1891 *Scaphites geinitzii* var. *binodosa* A. Römer; Jahn : 180, figs 1–5.
1907 *Scaphites Geinitzi* var. nov. *intermedia* Scupin : 696 (*nom. nud.*).
1913 *Scaphites Geinitzi* var. *intermedia* Scupin : 98.
1934 *Scaphites geinitzi* d'Orb. var. *intermedia* Scupin; Andert : 400.

TYPE. The references by Scupin (1907 : 696, 704) are insufficient to characterize this form and since there is no figure or reference to a previous figure or description the name at this date is a *nomen nudum*. However, in 1913 Scupin gave a long description of this variety and of the typical form of *S. geinitzii*, together with a reference for *intermedia* to a figure of Jahn's. The name is therefore established from this date. Scupin's description is by no means clear but he apparently knew a number of specimens from various localities which he regarded as belonging to his var. *intermedia*.

I designate here as **lectotype** of the subspecies *intermedius* Scupin the original of Jahn's figures (1891 : 180, 181, figs 1–5, described as '*Scaphites Geinitzii* var. *binodosa* A. Römer').

DESCRIPTION. Moderately compressed to inflated with strong rounded or bullate ventrolateral tubercles on shaft and hook, sometimes also on latter part of spire, and distinct umbilical bullae on the shaft. The primary ribs are only moderately strong.

REMARKS. Scupin rightly regarded his variety as a transitional form between typical *geinitzii*, with ventrolateral tubercles only, and *lamberti* Grossouvre, with umbilical tubercles as well which are more prominent than the ventrolateral ones. Those specimens with umbilical tubercles approximately as large as the ventrolateral ones, such as the *S. geinitzii* var. *binodosa* of Fritsch (which Grossouvre included in his *S. lamberti*), were treated by Scupin as transitional between *geinitzii intermedius* and *lamberti*. On the sole basis of the proportions of the tubercles this might be reasonable, but it appears to be more useful to take other features into account as well. Typical Coniacian *S. lamberti* are characterized by very coarse, well-separated secondary ribs, springing on the shaft and hook in pairs from the ventrolateral tubercles. *S. g. intermedius* has closer and finer ribbing than this, as do all *S. geinitzii*, with at least three secondaries to each ventrolateral tubercle.

OCCURRENCE. This subspecies does not occur in the Chalk Rock but seems to be widespread in the Upper Turonian of south Germany and Czechoslovakia.

Scaphites geinitzii laevior subsp. nov.

Pl. 3, figs 8, 9; Pl. 7, fig. 7

1872 *Scaphites Geinitzii* d'Orbigny; Schlüter : pl. 23, figs 21 and ? 22 only.
1895 *Scaphites Geinitzi* d'Orbigny; Jahn : 133; pl. 8, fig. 3a–d.

TYPES. The holotype is SM B594 from Reed, and paratypes are SM B4208, 21298 and 21300 from Cuckhamsley, and IGS Zr 7788 from Kensworth.

NAME. 'Smoother'.

DESCRIPTION. The density of the ribs on the spire is as much as twice that of the typical subspecies; the primary ribs on the shaft are less flattened and the ventrolateral bullae on the hook are thin and reduced. The greater rib density is owing partly to an increased number of primaries and partly to each primary being split into secondaries.

AFFINITIES AND DIFFERENCES. *S. planus* Roman & Mazeran (1913 : 13; pl. 4, figs 15–17) is a compressed and fine-ribbed form of the *geinitzii* group but the few small specimens on which the species was based are so poorly preserved that it is impossible to make out their characters adequately. If further material indicates that they are identical with *S. geinitzii laevior* the subspecific name should be changed to *planus*.

OCCURRENCE. This is a rather rare form in the Chalk Rock of Berkshire, Hertfordshire and Bedfordshire and in the *H. planus* Zone of Surrey; it occurs also in Germany.

Scaphites kieslingwaldensis Langenhan & Grundey

Pl. 3, figs 10–12

1891 *Scaphites kieslingwaldensis* Langenhan & Grundey : 9; pl. 1, fig. 1.
1897 *Scaphites binodosus* Römer; Fritsch : 37, fig. 20.
1901 *Scaphites kieslingwaldensis* Langenhan & Grundey; Sturm : 61; pl. 3, fig. 8.
1913 *Scaphites kieslingwaldensis* Langenhan & Grundey; Scupin : 101.
1934 *Scaphites kieslingwaldensis* Langenhan & Grundey; Andert : 402; pl. 19, fig. 5.

DESCRIPTION. This species is an inflated development of *S. geinitzii* with rounded rather than bullate ventrolateral tubercles on shaft and hook. Both the spire and the shaft are very inflated, the thickness being from 25% to 30% greater than in *S. geinitzii*; the whorl section of the spire may be almost circular; the venter of the hook is broad and in some examples nearly flat. Distinct rounded ventrolateral tubercles, varying in position from a half to two-thirds up the side, appear on the hook but are not in all cases clearly defined on the shaft. On the spire the primary ribs are rather thin and high, normally rectiradiate, rarely slightly sinuous and branch into two or three secondaries. On the shaft they are broad and blunt, varying in strength from weak to very prominent and, after a more or less distinct ventrolateral tubercle, each gives rise to three moderately strong secondaries.

The holotype has twice been refigured photographically. Fritsch's figure (1897 : 37, fig. 20) gives a clear idea of the species, but that of Sturm (1901 : pl. 3, fig. 8), perhaps the most accessible, is much retouched and gives a false impression of sharpness and narrowness of primary and secondary ribs.

AFFINITIES AND DIFFERENCES. The inflated members of the *geinitzii* group have generally in the past been referred to F. A. Römer's Campanian *S. binodosus*, which is bigger, less inflated and has ventrolateral tubercles already on the spire, while on the shaft they form a row of close prominent clavi. The Campanian *S. inflatus* Schlüter differs from *binodosus* only in having less clavate tubercles and in being more inflated, but the tubercles on the spire readily distinguish it from any of the Turonian group. Sturm, Scupin and Andert all treated *S. kieslingwaldensis* as a senior synonym of *S. meslei* Grossouvre, but that species has distinctly clavate ventrolateral tubercles on shaft and hook. Moreover, both *S. meslei* and *S. lamberti* Grossouvre, which does have rounded ventrolateral tubercles, are less inflated and have coarser ribbing than *S. kieslingwaldensis*. However, it may well turn out if more material becomes available that *lamberti* and *meslei* should be treated as subspecies of *kieslingwaldensis*. It is close to *geinitzii* and it is difficult to draw the line between the variable forms of the two species.

REMARKS. There is considerable variation in the appearance of these small inflated *Scaphites*, deriving mainly from variation in the straightness or sinuosity of the ribs and the position on the flanks of the ventrolateral tubercles. There also seems to be a tendency for earlier forms to have distinct tubercles only on the hook, while later examples have them also on the shaft, but too few specimens from different localities and horizons are known for one to be sure. For the present I would regard all these variable specimens as belonging to a single species.

OCCURRENCE. Rather rare in the Chalk Rock of Berkshire and Hertfordshire; it occurs also in central and northern Europe.

Scaphites lamberti Grossouvre

1894 *Scaphites Lamberti* de Grossouvre 241: pl. 32, figs 1, 5.

DESCRIPTION. A coarsely ribbed form with prominent bullate or circular ventrolateral and bullate umbilical tubercles on the shaft and hook. The ventrolateral tubercles may appear already on the last part of the spire. The ribs on the shaft are very strong and for the most part give rise to pairs of coarse, distant secondaries. The nominate subspecies, from the Coniacian, has strong umbilical tubercles and does not occur in England.

Scaphites lamberti doylei subsp. nov.

Pl. 3, fig. 13

? 1872 *Scaphites* sp.? Schlüter : 76; pl. 23, figs 23–25.
1934 *Scaphites lamberti* Grossouvre; Andert : 402; pl. 19, fig. 4a, b.

HOLOTYPE. BM C79486 from the Chalk Rock of Hitch Wood.

NAME. For Mr J. C. Doyle.

DESCRIPTION. The ribbing is similar to that of the typical Coniacian subspecies but with relatively feeble umbilical tubercles. Although this form is transitional between the more closely ornamented specimens of *S. kieslingwaldensis* and *S. lamberti* it has the characteristic ribs and general aspect of the latter.

AFFINITIES AND DIFFERENCES. *S. g. intermedius* is a comparable form but combines distinct umbilical tubercles with rather fine ventral ribbing. The spire figured by Jahn (1895: pl. 8, fig. 1a–d) as *S.* cf. *geinitzii* var. *lamberti* Grossouvre, from the Priesen Beds, seems to be a good deal more inflated and to have tubercles earlier than the English form. Schlüter's *Scaphites* sp. (1872 : pl. 23, figs 23–25) may perhaps be referable to this subspecies. On the other hand, the figures give the impression of clavate ventrolateral tubercles; if they are accurate, the specimen probably belongs to a parallel subspecies of *S. meslei* Grossouvre.

OCCURRENCE. It appears to be rare in the English Chalk Rock; the single undoubted specimen comes from Hitch Wood.

Scaphites diana sp. nov.

Pl. 3, figs 14–16

TYPES. The holotype is SM B21299; paratypes are SM B4225, B4239, B21301, BM C79515, J. C. Doyle coll. 645 and GSM 108906–7.

NAME. From Diana of Ephesus, the 'many-breasted mother'.

DESCRIPTION. A compressed to slightly inflated and evolute *Scaphites* with sinuous primary ribs on the shaft and about twelve pointed ventrolateral tubercles on the shaft and hook. On the spire the ribbing is rather irregular; the distant, low, regular rounded and sinuous primaries split high up on the sides into two low secondaries which cross the venter with a forward bend.

Affinities and differences. This rather uncommon species is readily distinguished from all subspecies of *S. geinitzii* by the open umbilicus, which is hardly occluded at all by the beginning of the shaft, and by the sinuous primaries, curling back to the abundant ventrolateral tubercles. On the shaft and hook the primaries are markedly flattened and sinuous, curving back to the small but distinct ventrolateral tubercles and then branching into three to five secondaries which cross the venter transversely. The evolute spire and the ribbing on the spire somewhat resemble that of contemporary *Otoscaphites* but the tubercles are very distinct. *S. compressus* d'Orbigny from the Lower Coniacian of France (Sornay 1956) is similar and is probably a direct descendant of *S. diana*. It differs primarily in having finer and denser ribbing on the spire, and, above all, a prominent row of rounded umbilical tubercles on the shaft.

Occurrence. Rather rare in the Chalk Rock of Cuckhamsley, Berkshire, Hitch Wood and Reed, Hertfordshire and Underwood Hall, Cambridgeshire.

Scaphites pseudoaequalis Yabe

Pl. 3, fig. 5; Pl. 7, fig. 1

1896 *Scaphites geinitzi* d'Orbigny; Woods : 81; pl. 3, figs 5, 5a only.
1910 *Scaphites pseudoaequalis* Yabe : 163; pl. 15 (1), figs 1–3.

Description. Small inflated *Scaphites* with well-spaced, slightly recurved primary ribs, splitting on the outer third of the side into two to four secondaries which run straight across the venter. On the shaft both primaries and secondaries become relatively stronger and more distant. On the hook the outer ends of the primaries project slightly and almost form ventrolateral tubercles. There is a wide constriction and a very strong flat-topped collar before the aperture. Of the external suture all the major elements are distinctly bifid except for the second lateral lobe.

Affinities and differences. The only comment that Woods made on his single specimen of this species was that 'in one small specimen the aperture of the shell has a projecting lip'. However, his specimen is rather distinct in proportions as well as in the aperture and is readily separated from all forms of *S. geinitzii*, particularly by the absence of any distinct ventrolateral tuberculation on the shaft.

Occurrence. Yabe's specimens from the *Scaphites* Beds of Hokkaido are probably of Lower Coniacian date. Woods' specimen came from Cuckhamsley (SM B4205) and two more have since been found by M. J. Oates at Kensworth (including GSM 115259).

Subfamily **OTOSCAPHITINAE** Wright, 1953

This subfamily was erected for *Worthoceras* Scott and (*pace* Wiedmann, 1965) its derivative *Otoscaphites* Wright, small lappeted scaphitids more evolute and with a simpler suture and ornament than their unlappeted contemporaries. They range from low in the Upper Albian to the Coniacian and it is only in the latter stage that they exhibit any significant tuberculation. *Worthoceras* is known in the Upper Albian only from Texas but in the Cenomanian and Turonian it is widespread in North America and occurs in Europe, north Africa and New Zealand. *Otoscaphites*, arising in the Cenomanian, extends the range of the subfamily to include eastern Asia, New Zealand and California.

Genus ***OTOSCAPHITES*** Wright, 1953

Type species. *Ammonites* (?) *bladenensis* Schlüter.

Otoscaphites bladenensis (Schlüter)

Pl. 3, figs 19, 20

1871 *Ammonites* (?) *bladenensis* Schlüter : 30; pl. 10, figs 5, 6.
1872 *Scaphites auritus* Schlüter : 77; pl. 23, fig. 9 only.

1875 *Ammonites Bladenensis* Schlüter; Barrois : 188.
1875 *Scaphites auritus* Schlüter; Geinitz : 192; pl. 35, fig. 10.
1925 *Scaphites bladenensis* (Schlüter) Diener : 197.
1945 *Scaphites auritus* Schlüter; Wright & Wright : 126; pl. 5, figs 1, 2.
1951 *Scaphites bladenensis* (Schlüter); Wright & Wright : 13.
1953 *Otoscaphites bladenensis* (Schlüter) Wright : 475.
1957*a* *Otoscaphites bladenensis* (Schlüter); Wright : 807.
1965 *Scaphites* (*Otoscaphites*) *bladenensis* (Schlüter); Wiedmann : 430; pl. 58, figs 2–4, 6.

LECTOTYPE. The original of Schlüter's (1871) pl. 10, figs 5, 6 (Wright 1957*a* : 807).

DESCRIPTION. Rather small with a very evolute spire, a short straight or curved shaft and a hook; the ends of the lappets overlap the spire. The whorl section of the spire is moderately compressed with gently convex sides and a narrowly rounded venter; there may be rather strong bifurcating sigmoid ribs, which bend forward slightly on the venter, giving the appearance of a *Deshayesites*, or the primaries may only be visible on the inner half of the side. Towards the end of the spire the umbilical shoulder, hitherto rounded, becomes sharper and on the shaft and hook it is distinctly angular; between it and the dorsal impression there is a distinct flat bevel. The sides of the shaft are flat and on shaft and hook the ribbing is weak and irregular; very feeble rounded or flat primary ribs spring at a forward angle from the umbilical shoulder, quickly straighten and run radially to the ventrolateral shoulder where they may break into very feeble fine riblets or continue as obscure folds over the venter. At least in some specimens the periphery of the shaft and hook is not evenly curved but is made up of a series of short straight lengths. The aperture is preceded by a marked constriction and a high collar, vertical behind and sloping in front; there are long, parallel-sided lateral lappets, slightly turned up.

AFFINITIES AND DIFFERENCES. When my brother and I described two Surrey specimens as *Scaphites auritus* (Wright & Wright 1945), we included in a single species all the specimens figured by Schlüter (1872) as *S. auritus* and also those figured in the same year by Fritsch and described homonymously as *S. auritus*. Grossouvre (1894 : 243) had already renamed Fritsch's specimens *S. fritschi*, distinguishing them from Schlüter's *S. auritus* on the grounds that the ribs were less flexuous and more distant on the inner part of the side. In fact Schlüter's three specimens are all different; only one of them has close flexuous ribs (1872 : pl. 23, figs 7, 8) and this specimen is closely paralleled by one of Fritsch's (1872 : pl. 13, fig. 14). The other specimens on Fritsch's pl. 13 are poorly preserved or consist only of the spire, while his pl. 14, fig. 12 represents a lappeted *Scaphites* of normal type. The *Otoscaphites* figured by Jahn (1895 : pl. 8, fig. 5a–d) as *S. fritschi* Grossouvre is incomplete and does not help to clarify the characters of that species, if indeed it belongs to the same species as Fritsch's specimens. By distinguishing the various forms and by designating lectotypes appropriately it is possible to make sensible use of all the available names. I have already designated as type of *Ammonites* (?) *bladenensis* Schlüter the original of his pl. 10, figs 5, 6. Wiedmann has (1965 : 429) pointed out that of Schlüter's three specimens of '*S. auritus*' only that figured in his pl. 23, fig. 9, is identical with *bladenensis*. Wiedmann also designated as lectotype of *Scaphites auritus* Schlüter the original of his pl. 23, figs 5, 6; this species is characterized by its sharp umbilical tubercles from which spring directly bundles of three straight ribs. I do not agree with Wiedmann that Schlüter's third specimen belongs to the same species; indeed he points out that in this, the 'presumed paratype', there are no tubercles. This specimen, as Wiedmann says, is identical with the original of Fritsch's pl. 13, fig. 14, which I hereby designate as **lectotype** of *Scaphites auritus* Fritsch, a homonym of *S. auritus* Schlüter, and thereby of its replacement nominal species *S. fritschi* Grossouvre. This same species, *S. fritschi*, is characterized by rather sinuous, very fine and close ribs on the shaft and slightly coarser ribs on the hook which at first branch into two or three secondaries but are finally single; it is probably closer to *O. reidi* sp. nov. (see p. 307) than it is to *O. bladenensis*.

O. reidi has a further distinctive type of ribbing consisting of very distinct but fine prorsiradiate primaries, each giving rise two-thirds up the side to two to four very fine secondaries that cross the venter almost transversely. *O. awanuiensis* Wright from New Zealand has a well-rounded whorl section even on the shaft, but rather depressed and coronate on the spire, and fine rather distant primary ribs branching regularly into three secondaries on both spire and shaft. It is not, however, 'undoubtedly Upper Turonian' as I stated in 1954; Mr H. Wellman subsequently sent me a well-preserved specimen which was found in association with *Hypoturrilites* and *Scaphites* cf. *equalis* Sowerby of Cenomanian date. Henderson (1973) described and figured further Cenomanian material.

The Japanese Coniacian *O. puerculus* (Yabe) (1910 : pl. 15) and its var. *teshioensis* (Yabe), with spire rather like that of *O. bladenensis*, have prominent primary ribs on the shaft which extend to the ventrolateral shoulder before subdividing; in the var. *teshioensis* there are distinct ventrolateral tubercles at the point of branching. *O. minutus* (Moreman), from the basal Turonian of the western interior of the U.S.A., has a whorl section much like that of *O. awanuiensis*, but much weaker ribs on shaft and hook and lappets splayed sideways. *O. arnaudi* (Grossouvre) is at once distinguished from all other species by having very sinuous branching ribs of more or less the same type on spire, shaft and hook.

OCCURRENCE. *O. bladenensis* appears to be widely distributed in England and rather common in places, mainly in the nodular facies of the *Holaster planus* Zone in Kent and Surrey, but it also occurs rarely in the Chalk Rock of Hitch Wood. It occurs in Germany and Czechoslovakia.

Otoscaphites reidi sp. nov.

Pl. 3, figs 17, 18; Pl. 7, fig. 8

1957*a* *Otoscaphites* sp. ('third undescribed European form') Wright : 807.

TYPES. The holotype is IGS Zr7952 from High Wycombe. Paratypes are BM C79498 (WW *ex* Reid coll.) from Medmenham, BM C79511–4 (WW coll.) and Doyle coll. 228 from Hitch Wood, and IGS Zr 7789 (Payne & Hogg coll.) from Kensworth.

NAME. For Mr R. E. H. Reid.

DESCRIPTION. The spire has weak, well-spaced, rounded ribs that branch indistinctly. The shaft is flat-sided with broadly rounded venter and is rather long; very distinct sharp primary ribs leave the sharp umbilical shoulder at a forward angle of about 45° forming a very slight tubercle at the edge; a quarter of the way up the side they turn sharply to a radial direction; at midflank they break into two or three fine close and slightly sinuous secondaries which, with occasional intercalatories, cross the venter transversely. The hook expands rather rapidly until it is as wide as or wider than high, with rather flattened venter; here the primary ribs are sinuous and the secondaries more numerous and finer, in some parts absent. The apertural margin is well shown in the holotype and has the typical constriction, collar and long lateral lappets of *Otoscaphites*.

AFFINITIES AND DIFFERENCES. None of the species distinguished above under *O. bladenensis* have ribbing on the shaft like that of *O. reidi*. *O. bladenensis* itself is more compressed and has very feeble, blunt, rounded and more or less radial primaries on the shaft with fine almost obsolete secondaries. The specimen figured by Yabe (1910 : pl. 15, fig. 24), described as *O. puerculus* var. *teshioensis*, has a close resemblance to *O. reidi* but is characterized by ventrolateral tubercles lacking in *O. reidi*. *O. puerculus* itself, if interpreted solely by the lectotype (Jimbo 1894 : pl. 21, fig. 4, selected by Matsumoto, 1963 : 44), would seem to be very distinct from *O. reidi*, but Tanabe (1975) has recently demonstrated an evolutionary series in *O. puerculus* in presumed Middle Turonian, of which the earlier members (e.g. his pl. 10, figs 1, 2) are close to *O. reidi*. However, these *O. puerculus* seem to have a much less flat-sided shaft with sharper and more crescentic primary ribs and less distinct and regular secondaries than *O. reidi*.

OCCURRENCE. Chalk Rock of Buckinghamshire, Hertfordshire and Bedfordshire.

Family **DESMOCERATIDAE** Zittel, 1895

Subfamily **PUZOSIINAE** Spath, 1922

Genus ***PUZOSIA*** Bayle, 1878

TYPE SPECIES. *Puzosia subplanulata* (Schlüter).

It has been held that true *Puzosia* did not survive the end of the Cenomanian, and Turonian forms have consequently been attributed to *Austiniceras* or some other genus. However, several good species of the genus have been described from the Turonian of various parts of the world; most were referred to by Matsumoto in his paper on the Puzosiidae of Hokkaido and Saghalien (1954). Too few specimens have been collected yet for distinctions to be drawn with certainty or for time-ranges to be worked out for the various species.

Puzosia curvatisulcata Chatwin & Withers

Pl. 4, fig. 4; Pl. 7, fig. 3

? 1898 *Puzosia gaudama* (Forbes); Kossmat : 115; pl. 16, fig. 2a, b only.
1909 *Puzosia curvatisulcata* Chatwin & Withers : 68; pl. 2, figs 1–4.
1913 *Puzosia gaudemarisi* Roman & Mazeran : 19; pl. 2, figs 1, 1a, 2, 2a.
1922 *Austiniceras* (?) *curvatisulcatum* (Chatwin & Withers) Spath : 128.
1951 *Austiniceras* (?) *curvatisulcatum* (Chatwin & Withers); Wright & Wright : 19.
1954 *Puzosia orientale* Matsumoto : 74; pl. 13, figs 1, 2a, b.
? 1954 *Puzosia orientale kossmati* Matsumoto : 75.
? 1959 *Puzosia intermedia orientalis* Matsumoto; Matsumoto : 16; pl. 4, fig. 1a–c.

TYPES. The two syntypes, BM C12229a and b, from the Chalk Rock of Marlow, are probably fragments of one individual. In case of doubt, I select the larger fragment (C12229a) as **lectotype**.

DESCRIPTION. Probably very large; the largest Chalk Rock specimen seen has a diameter of about 160 mm and the holotype of *P. gaudemarisi* figured by Roman & Mazeran (1913 : pl. 2, fig. 1, 1a) has a diameter of 180 mm, but a fragment (BM C79656) from the *Holaster planus* Zone that probably belongs to this species is still septate at an estimated diameter of about 380 mm. Moderately compressed, the whorl thickness varying from 70% to 80% of whorl height; the greatest breadth is at about one-third of the whorl height. The umbilical wall is steep but rounded; the sides are flatter on early and more rounded on later whorls. On internal moulds there are visible five or six constrictions to a whorl, radial or slightly prorsiradiate on the inner part then curving moderately far forward and crossing the venter in a rounded arc. The strength of the constrictions varies slightly with age and between individuals. Fine, weak ribs are visible on the outer part of the sides and on the venter on internal moulds. On the shell the constrictions have a strong rib in front and many of the intermediate ribs arise on the umbilical shoulder even at small diameters.

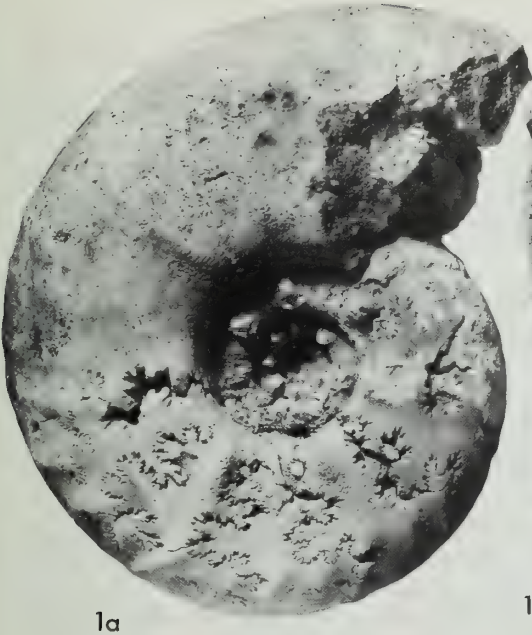
AFFINITIES AND DIFFERENCES. The specimen figured in Pl. 4, fig. 4 (BM C79501) was identified by Matsumoto as 'closely allied to the inner whorl of *Puzosia* (s.s.) *orientale* Matsumoto [= *P. gaudama* Kossmat 1898, *non* Forbes] from Japanese Neogyliakian: Turonian; also resembling *P. curvatisulcata* Chat. & With. which has a more strongly impressed constriction and *P. mulleri*

Plate 4 ×1

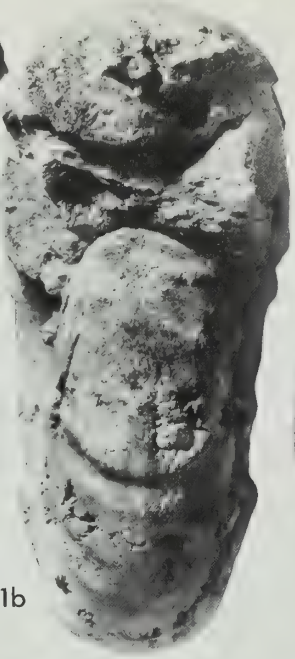
Lewesiceras mantelli Wright & Wright (p. 310). Hitch Wood.
Figs 1a, b, 2, 3. Coll. R. E. H. Reid, BM C79481, C79500, C79480. See also Pl. 6, figs 4–5.

Puzosia curvatisulcata Chatwin & Withers (above). Blount's Farm Pit, Marlow.
Fig. 4. Coll. R. E. H. Reid. BM C79501. See also Pl. 7, fig. 3.

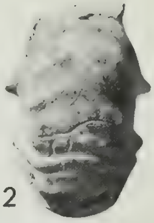
Pseudojacobites farmeryi (Crick) (p. 313). Hitch Wood.
Fig. 5. Coll. C. J. Wood. IGS Zr 7977. See also Pl. 5, fig. 1a, b (same specimen) and Pl. 6, figs 2–3. See Fig. 2, p. 313, for suture.



1a



1b



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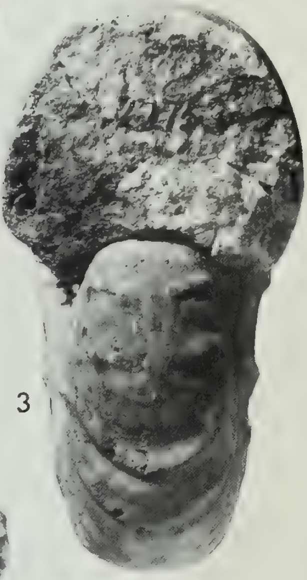

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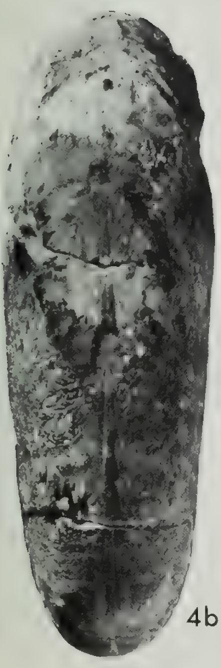
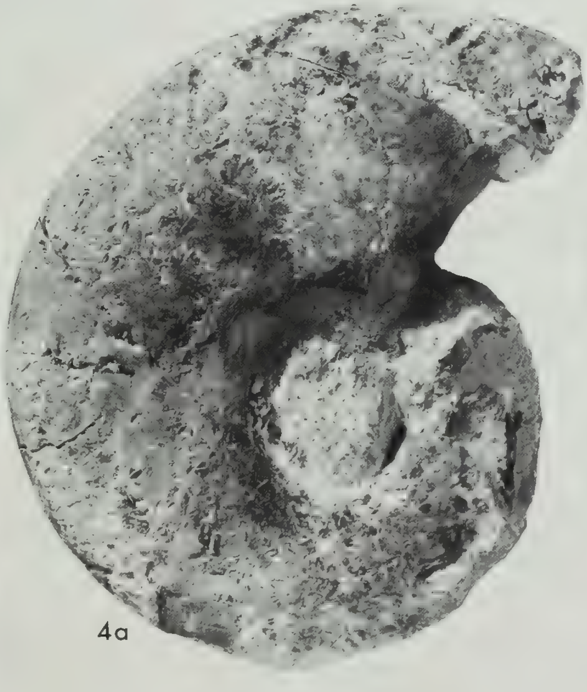
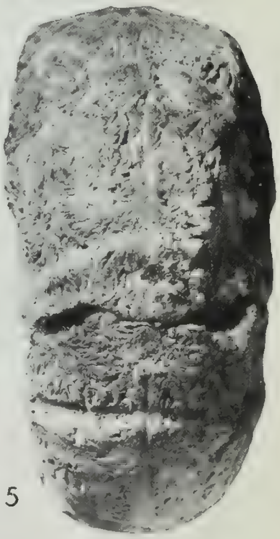


4b



4a



5

Gross., which is more compressed'. Better English material is now available than the two poorly-preserved fragments figured by Chatwin and Withers. Allowing for even a modest amount of variation in the strength of the constrictions and the proportion of height to breadth of whorl, both of which seem to change with growth, it seems to me impossible to maintain the specific distinction of *P. orientalis* and *P. curvatisulcata.* At the most it may be desirable to distinguish a Lower Turonian subspecies *P. c. orientalis* from an Upper Turonian *P. c. curvatisulcata*, but I doubt it. *P. intermedia kossmati* Matsumoto seems to differ sufficiently, in its more extreme forward bending of the ribs and constrictions on the outer part of the sides and in the sharper, denser ribbing, to be treated as a distinct subspecies of *curvatisulcata. P. intermedia* Kossmat I would treat as a distinct species on the basis of the precocious appearance of long ribs already at a diameter of 55 mm and their falcoid course. *P. gaudemarisi* Roman & Mazeran cannot in my view be distinguished from *P. curvatisulcata.*

OCCURRENCE. Rather rare in the Chalk Rock of Blount's Farm pit, Marlow, Hitch Wood and Kensworth; occurs also in the Upper Turonian of Uchaux, France and the Lower Turonian of southern India, Japan and California.

Family **PACHYDISCIDAE** Spath, 1922

Genus ***LEWESICERAS*** Spath, 1939

TYPE SPECIES. *Ammonites peramplus* Mantell, 1822.

Lewesiceras is characterized by its strong but irregular ribbing on the early whorls, the ribs bent forward ventrolaterally, with constrictions and umbilical tubercles; the ornament tends to weaken on later whorls except for distant bar-like primary ribs. The sutures are well spaced with minutely frilled elements and widely splayed lobes.

The Turonian *Ammonites peramplus* Mantell was long regarded as typical of the family Pachydiscidae, but Spath rightly separated as *Lewesiceras* the Turonian species with strongly ribbed and tuberculate inner whorls from the restricted *Pachydiscus* of the Campanian and Maastrichtian. Houša (1967) has reviewed *Lewesiceras* and distinguished two groups previously included in it, *Menabonites* and *Tongoboryoceras*; the latter occurs in the Chalk Rock (see p. 316).

The genus ranges probably from the Cenomanian (*Lewesiceras* ? sp. from Algeria, figured as *Pachydiscus* sp. – Pervinquière 1910 : 37; pl. 3, figs 1, 2) to the Upper Turonian and perhaps Coniacian.

Lewesiceras mantelli Wright & Wright
Pl. 4, figs 1–3; Pl. 6, figs 4, 5

1850 *Ammonites prosperianus* d'Orbigny; J. de C. Sowerby : 359; pl. 27, fig. 22.
1853 *Ammonites peramplus* Mantell; Sharpe (*pars*) : 26; pl. 10, figs 2, 3a, b only.
1870 *Ammonites peramplus* Mantell; C. F. Römer : 319; pl. 35, fig. 5.
1872 *Ammonites peramplus* Mantell; Schlüter : 31; pl. 10, figs 7–14.
1872 *Ammonites peramplus* Mantell; Fritsch : 38; pl. 8, fig. 4 only.
1874 *Ammonites peramplus* Mantell; Geinitz : 189; pl. 34, figs 5, 6, ? 4.
1896 *Pachydiscus peramplus* (Mantell) Woods : 79.
1913 *Pachydiscus peramplus* Mantell (Sowerby); Roman & Mazeran : 14; pl. 1, fig. 2 only.
1913 *Pachydiscus vaju* Stoliczka; Roman & Mazeran : 16; pl. 1, figs 5–9.
1926 *Pachydiscus cricki* Spath : 82 (*non* Kossmat 1898).
1927 *Pachydiscus sharpei* Spath; Billinghurst : 514; text-fig. 2a–c.
1951 *Lewesiceras mantelli* Wright & Wright : 20.
1952 *Lewesiceras mantelli* Wright; Collignon : 84 (republished 1955 : 78).
1958 *Lewesiceras peramplus* (Mantell); Drushchitz, Michailov & Eristavi : pl. 52, fig. 2a–c.
1959 *Lewesiceras peramplum* (Mantell); Najdin & Shimanskij : 185; pl. 12, fig. 4a–c; pl. 13, fig. 4a, b.
1964 *Lewesiceras romani* Sornay : 183, text-figs 1–4.
1967 *Lewesiceras mantelli* Wright & Wright; Houša : 26; pl. 4, fig. 3 only; pl. 5, figs 1–4; ? pl. 6, figs 1–4.
1967 *Lewesiceras lenesicense* Houša : 35; pl. 8, figs 1–7.

TYPE. *L. mantelli* was a *nom. nov.* for *Pachydiscus cricki* Spath, 1926 (*non* Kossmat, 1898), of which the holotype by monotypy is BM 88587, the original of Sharpe, 1853 : pl. 10, fig. 3a, b.

DESCRIPTION. Small (*c.* 90 mm diameter) to moderate in size, rather involute, the section depressed and coronate in the young but becoming higher with growth, varying from inflated and rounded on the body chamber to slightly compressed. To a diameter of 50 to 60 mm the umbilicus is surrounded by large and prominent laterally-directed spines (rounded tubercles on internal moulds) on the edge of the vertical umbilical wall, commonly six or seven to a whorl. The first distinct tubercle normally appears at a diameter of 11 mm and the second at 15 mm. From each spine branch two or three ribs, frequently with a marked constriction in front of the strongest. Shorter ribs are irregularly intercalated. All ribs tend to be weak on the inner part of the side and strongest on the shoulder where they may be angulate or rarely almost form tubercles (Pl. 4, fig. 2). Specimens with the more angulate shoulders naturally have a squarer whorl section than the normal ones. The ribs curve forward strongly and the more prominent ones, particularly those associated with constrictions, form distinct tongue-shaped ridges on the venter.

From a diameter of about 60 mm the whorl is as high as wide, the umbilical spines become weaker and the ribs become more equal and less prominent. The last large spine normally appears at a diameter of about 65 mm, at which stage only the inner part of the ribs remain. At greater diameters there is normally little ornament except very weak umbilical bulges and faint swellings on the venter, but in some cases the ribs may persist ventrally to slightly greater diameters.

The sutures are well spaced and do not interlock; the saddles are plump, subquadrate and regularly and minutely frilled; the lateral lobes are rather wide and irregularly trifid; the external lobe is little more than half as long as the first lateral.

Specimens occur rarely with up to eleven umbilical spines (e.g. IGS 7981 from Hitch Wood and Zr 9329 from Kensworth – see Pl. 6, fig. 4); in fact in such specimens the number of umbilical tubercles is normal on the inner whorls and the excess number only arises at the beginning of the body chamber. The original of d'Orbigny's 1840 : pl. 100, figs 1, 2 is perhaps such a form. A few specimens are known (e.g. BM 88709; Pl. 6, fig. 5) with stronger, sharper and more regular ribs, resembling those of some *Nowakites* or even *Canadoceras*.

AFFINITIES AND DIFFERENCES. Distinction from the earlier *L. peramplum* is difficult because that species is known mainly from very large, badly-preserved specimens. An individual of 60 mm diameter from the *Inoceramus labiatus* Zone of Wharram, North Humberside (WW 9311, *ex* Stainforth coll.) accords reasonably well with the small *L. peramplum* figured by Houša from the Lower Turonian of Czechoslovakia (1967 : pl. 1, figs 1, 2) and is intermediate between the inner whorls of the Upper Albian *Eopachydiscus laevicanaliculatum* (Römer) and the Upper Turonian *L. mantelli*. Compared with the latter it has somewhat more compressed and flatter-sided whorls, weaker umbilical tubercles, feebler constrictions and stronger and more regular intermediate ribs.

L. plicatum Houša (1967 : 32; pl. 7, figs 1–4) differs from the contemporary *L. mantelli* in being more compressed and in having denser ribs that persist with the juvenile sinuous character to a later stage. Certain undescribed Yorkshire specimens (WW 9310, 9313, *ex* Stainforth coll.) may be the inner whorls of *L. plicatum*.

L. sharpei (Spath, 1926 : 82) was based on one of Sharpe's figures of *Ammonites peramplus* (1853 : pl. 10, fig. 1a, b only). This figure, reduced to half natural size, is of a large but incomplete, rather compressed *Lewesiceras* with twelve weak umbilical bulges on the last-preserved whorl, but no other ornament; the inner whorls are missing. The specimen is quite unfit for the diagnosis of a species in this genus; it has not been traced and its precise horizon is unknown. *L. sharpei* (Spath) should be treated as a *nomen dubium*. Wright & Wright (1951 : 20) were wrong to include the original of Sharpe's pl. 10, fig. 2 in *L. sharpei*; it is in fact a typical *L. mantelli*.

The abundant Uchaux examples identified by Roman & Mazeran (1913) as *Pachydiscus vaju* (Stoliczka) and described as a new species *L. romani* by Sornay (1964) seem to be typical examples of *L. mantelli*; the stated grounds for distinction from *L. mantelli* were the more depressed whorl section and more numerous, rounded and prominent umbilical tubercles, but in these and all other features the Uchaux specimens fall within the range of *L. mantelli*. *P. vaju* itself is a Santonian species and probably a *Nowakites*.

The Malagasy *L. beantalyense*, *L. sornayi* and *L. tongoboryense* described by Collignon (1952, =1955) all have much more rounded whorl sections than *L. mantelli* and have been separated from *Lewesiceras* by Houša (1967) as *Tongoboryoceras* (see p. 316), while the Indian *Pachydiscus anapadensis* Kossmat and the Malagash *L. masiaposense* Collignon, both referred to *Lewesiceras* by Collignon (1952), are characterized by strong ventrolateral tubercles joined across the venter by fine looped ribs and have been placed by Houša in a new genus *Menabonites*.

Houša's (1967) *L. lenesicense* is based on small specimens, all figured enlarged, which are typical *L. mantelli*. His far larger specimens attributed to *L. mantelli*, many figured much reduced, may well belong to this species, but English material of the size of his largest specimens has not been found. That his interpretation of *L. mantelli* differs from mine can also be seen from a comparison of the specimens figured in the literature that are referred by each of us to this species, as indicated in our synonymies. However, some of the references to early nineteenth-century authors given in Houša's synonymy but omitted from mine may well refer to *L. mantelli*.

NOMENCLATURE. This species is widely quoted as *L. cricki* (Spath). Collignon (1952 : 84, =1955 : 78) objected, since the two species belong to different genera, to the renaming of the species because of the prior existence of *Pachydiscus cricki* Kossmat. He ignored however the fact that Spath established his species not as *Lewesiceras cricki* but as *Pachydiscus cricki*; such a primary homonym must under the Rules be renamed.

OCCURRENCE. This is the commonest and most widespread ammonite in the Chalk Rock and indeed in the rest of the *Holaster planus* Zone, occurring even in Lincolnshire and Yorkshire. It is widely distributed in Europe, being recorded usually as *Ammonites* or *Pachydiscus peramplus*. It also occurs in the *Terebratulina lata* Zone (WW 14054 from the Guildford bypass, Surrey).

Lewesiceras woodi sp. nov.

Pl. 3, fig. 21; Pl. 6, fig. 6

1973 *Pseudopuzosia* sp., Birkelund : 141; pl. 12.

TYPES. The holotype is BM C79509 (WW *ex* Reid coll.) from the Chalk Rock of Hitch Wood; paratypes are BM C20239 from the Chalk Rock of Aston Rowant, Oxfordshire, C79504 (WW coll.) presumably from the *Holaster planus* Zone and probably from Kent, and C79520 (Gaster coll.) from the *H. planus* Zone of Malling Hill, Lewes; also Birkelund's specimen MMH 12836, from Särdal, Sweden.

NAME. For Mr C. J. Wood.

DESCRIPTION. Rather compressed with distinctly flat subparallel sides and a low rounded venter. The ornament on the inner whorls is very feeble. There are eight or nine well-marked constrictions, radial on the inner part of the side, then curving forward but crossing the venter with only a slight bend. Behind each is a moderately strong rib, steep in front and shallow behind, raised into a slight bulla on the umbilical shoulder. Between constrictions there are two to four very feeble broad irregular ribs.

AFFINITIES AND DIFFERENCES. This species is obviously a *Lewesiceras* derived from the main stock by reduction of the umbilical tuberculation and the ribbing. In these respects it resembles the inner whorls of *Pseudojacobites* and *Tongoboryoceras* but is readily distinguished by its relative compression, flatter sides, strong forward bend of the constrictions and main ribs on the ventrolateral shoulders and by the well-spaced sutures typical of *Lewesiceras*. Birkelund's Sardal specimen has these sutures and, though more than twice as big as any of the English specimens, exhibits the characteristic features of *L. woodi*.

Occurrence. Rare in the Chalk Rock of Hertfordshire and Oxfordshire, in the *H. planus* Zone of ? Kent and Sussex and in the Upper Turonian of Särdal, Sweden.

Genus *PSEUDOJACOBITES* Spath, 1922
[*Pseudopuzosia* Spath, 1926; *Rotalinites* Shimizu, 1935]

Type species. *Pachydiscus farmeryi* Crick, 1910.

Moderately evolute, inflated with strong constrictions, behind each of which is a strong rounded rib springing from an umbilical bulla, and weak irregular intermediate ribs. On the outer whorls there are strong ventrolateral and siphonal tubercles. The sutures interlock to a slight extent and have long narrow highly-divided bifid saddles and trifid lobes (Fig. 2).

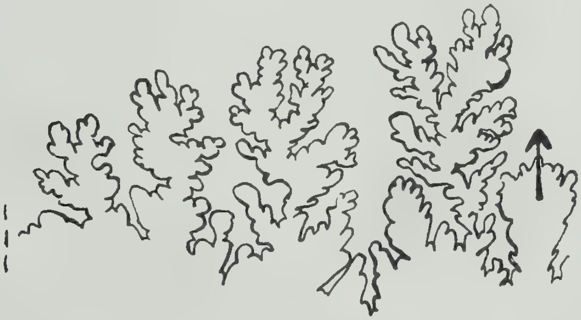


Fig. 2 Suture of *Pseudojacobites farmeryi* (Crick), ×2.

Study of two well-preserved specimens collected in recent years has surprisingly demonstrated that the holotype of *Desmoceras marlowense* Noble, the type species of *Pseudopuzosia* Spath, consists of the inner whorls of a specimen of *Pachydiscus farmeryi* Crick, the type species of *Pseudojacobites* Spath.

The genus is readily distinguished from *Lewesiceras* not only by the ventrolateral and siphonal tubercles on the outer whorls but also by the more depressed whorl section, straighter ribs and constrictions and the interlocking sutures with longer and narrower elements (cf. Fig. 2 and Pl. 5, fig. 1). The tubercles and the weaker, less regular ribbing distinguish *Pseudojacobites* from *Tongoboryoceras*.

Pseudojacobites ranges from Upper Turonian to Coniacian. The Santonian attribution of a species from Texas is doubtful. The genus is widespread but apparently always rare, occurring in Madagascar, southern India, Japan and Texas as well as England.

Pseudojacobites farmeryi (Crick)
Fig. 2; Pl. 4, fig. 5; Pl. 5, fig. 1; Pl. 6, figs 2, 3

1910 *Pachydiscus farmeryi* Crick : 345; pl. 27, figs 1, 2.
1911 *Desmoceras marlowense* Noble : 398, text-figs 1, 2.
1922 *Pseudojacobites farmeryi* (Crick) Spath : 121.
1926 *Pseudopuzosia marlowense* (Noble) Spath : 80.
1954 *Pseudopuzosia marlowensis* (Noble); Matsumoto : 113, text-fig. 5.

Types. The holotype, by monotypy, is BM C12220 from the *Holaster planus* Zone of Boswell, Lincolnshire; the holotype of *Desmoceras marlowense* Noble is GSM 25456.

Description. Moderately evolute whorl section, increasing very sharply, wider than high and widest at the umbilical shoulder, with long, very slightly convex umbilical wall, slightly flattened sides and broadly rounded venter. There are eight constrictions well marked on the internal mould, shallow and prorsiradiate on the umbilical wall, rectiradiate on the inner part of the side then curving very slightly forward to cross the venter in a very shallow arc or even transversely. Immediately behind the constriction and following the same course is a prominent well-rounded rib with a distinct large rounded-bullate tubercle on the umbilical shoulder. On the shell (partly preserved in GSM 108896) there is no constriction and the rib is stronger with a more bullate tubercle.

From a diameter of about 45 mm, both on mould and shell, a broad rounded ventrolateral tubercle appears irregularly on main and intermediate ribs, becoming increasingly strong with growth producing a squarish whorl section. Slightly later, there appears on the mould behind each constriction a low rounded tubercle on either side of the siphuncle; on the shell even at this stage there was probably a single transversely elongated siphonal tubercle.

REMARKS. Although the holotype of *Desmoceras marlowense* (Pl. 6, fig. 2a, b) is worn in places and scraped in others, it is by no means as poor a specimen as has been believed. It had in fact been coated with layers of varnish and casting compounds so that its details became obscured. Now cleaned, it can be seen to coincide in all respects with the corresponding stages of the well-preserved specimen figured in Pl. 5, fig. 1. The earliest traces of ventrolateral tubercles can just be seen on the abraded final part of the specimen.

Crick's holotype of *P. farmeryi*, once allowance is made for the lateral crushing and the fact that the specimen is a composite mould, compares very well with the original of Pl. 5, fig. 1. Further support for the identification of these specimens is provided by GSM 108896, which matches the holotype of *marlowense* and also has preserved a pseudomorph of part of the shell showing intermediate ribs like those of the holotype of *farmeryi*.

AFFINITIES AND DIFFERENCES. *Pseudojacobites* seems to be rare wherever it occurs and only a handful of foreign specimens is known – a few *P. rotalinus* (Stoliczka) from the Coniacian of south India and Madagascar, two specimens of *P. ankobensis* Collignon (1965) and two of *P. masiaposensis* (Collignon, 1965) from the Upper Turonian of Madagascar, and the holotype of *P. texanus* Matsumoto (1966) probably from the Turonian of Texas.

Of these *P. masiaposensis* (Collignon) (1955 : pl. 1, fig. 1; 1965 : pl. 380, fig. 1644) is very close to its contemporary *P. farmeryi*. It differs only in having much larger and more prominent tubercles, particularly the umbilical ones, and in its sharper and more regular doubled ribs on the venter. *P. ankobensis* Collignon (1965 : 10; pl. 380, fig. 1643), another contemporary, apparently has a more precocious development of the ventrolateral and siphonal tubercles, but the umbilical ones are perhaps smaller than in *P. masiaposensis*.

Plate 5 ×1 (Figs 8, 10 ×2)

Pseudojacobites farmeryi (Crick) (p. 313). Hitch Wood.
Fig. 1a, b. Coll. C. J. Wood. IGS Zr 7977. See also Pl. 4, fig. 5 (same specimen) and Pl. 6, figs 2–3. See Fig. 2, p. 313, for suture.

Subprionocyclus neptuni (Geinitz) (p. 319). Hitch Wood.
Figs 2a, b, 3a, b. Coll. R. E. H. Reid. BM C79519, C79655.

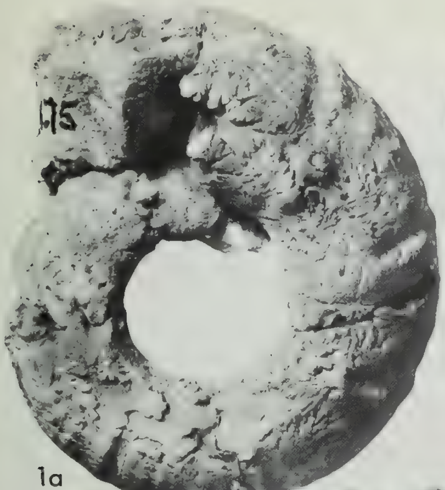
Subprionocyclus branneri (Anderson) (p. 320). Hitch Wood.
Fig. 4. Coll. WW. BM C79477. Figs 5a, b, 6a, b. Coll. R. E. H. Reid. BM C79483, C79482.

Subprionocyclus hitchinensis (Billinghurst) (p. 318).
Figs 7–10. Hitch Wood. Fig. 7, Coll. R. E. H. Reid. BM C79472. Figs 8–10, Coll. WW. BM C79495, ×2; C79484, ×1; C79654, ×2. Fig. 13. *Holaster planus* Zone, Guildford bypass. Coll. Mrs Suggate. BM C79474.

Subprionocyclus sp. (p. 320). Reed Quarry, near Royston.
Fig. 11a, b. Coll. C. J. Wood. GSM 108932.

Subprionocyclus normalis (Anderson) (p. 321). Hitch Wood.
Fig. 12a, b. Coll. WW. BM C79494. See also Pl. 7, fig. 2.

Photographs: Figs 5b and 12a by BM.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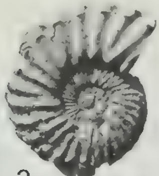
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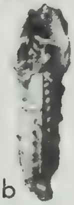
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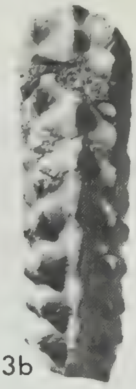
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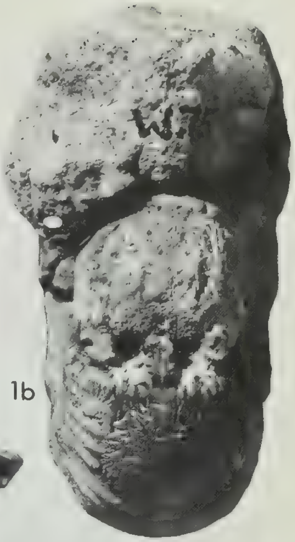
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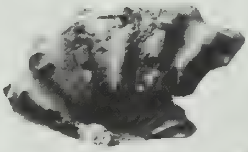
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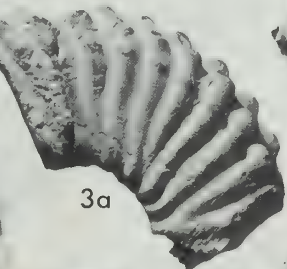
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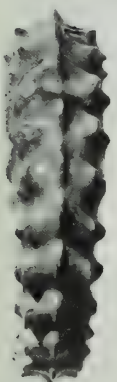
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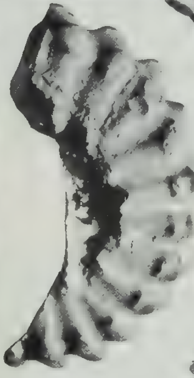
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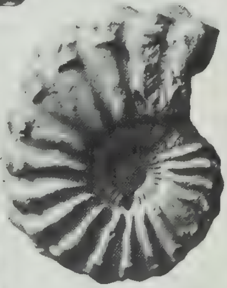
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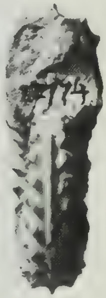
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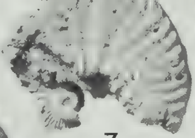
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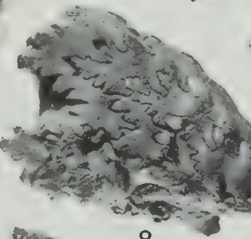
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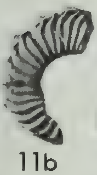
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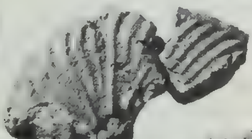
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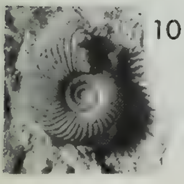
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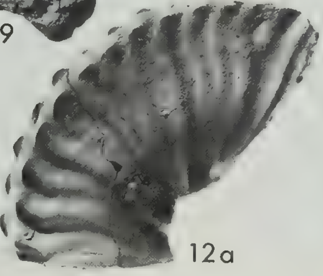
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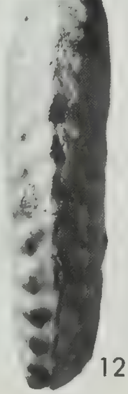
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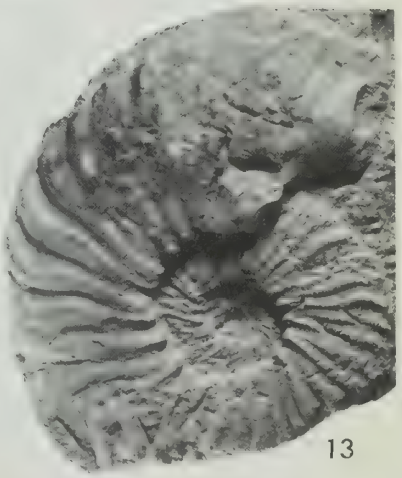
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The Coniacian *P. rotalinus* (Stoliczka) has a more circular whorl section, has ten or more, rather than eight, primary ribs, which are more regular and prominent, and loses the fine secondary ribs at a diameter probably of about 45 or 50 mm, after which there are a few irregular coarse secondaries.

P. texanus Matsumoto has a comparatively high whorl section, regular well-marked secondaries nearly as strong as the primaries and rather small tubercles.

Menabonites anapadensis (Kossmat) from the Coniacian of south India much resembles *Pseudojacobites masiaposensis* in its depressed whorl section and the ventrolateral tubercles on the outer whorl, but has no siphonal tubercles (see above, p. 312).

Occurrence. The holotype, BM C12220, from Boswell, Lincolnshire, is from normal chalk recorded as of the *Holaster planus* Zone; the remaining specimens come from the Chalk Rock of Hill End Farm pit, Hitch Wood and Blount's Farm pit, Marlow.

Genus *TONGOBORYOCERAS* Houša, 1967

Type species. *Lewesiceras tongoboryense* Collignon, 1952.

Houša (1967 : 42) rightly distinguished from *Lewesiceras* a group of species with uniform whorl section and more or less equal primary and secondary ribs. Study of the English specimens of *T. rhodanicum* Roman & Mazeran shows that there are other important generic characters. *Tongoboryoceras* shares with *Pseudojacobites* a complex suture with long and relatively narrow elements compared with those of *Lewesiceras*. The early whorls of *Tongoboryoceras*, moreover, are smooth to a much later stage than those of *Lewesiceras* and the strong constrictions form a marked angle on the venter.

Tongoboryoceras rhodanicum (Roman & Mazeran)

Pl. 6, figs 1, 7

1913 *Pachydiscus rhodanicus* Roman & Mazeran : 18; pl. 1, fig. 10a, b.
1954 *Pseudopuzosia marlowensis* Noble; Matsumoto : 113, text-fig. 6 only.
1967 *Tongoboryoceras rhodanicum* (Roman & Mazeran) Houša: 42.

Description. Rather involute, with depressed whorl section about twice as wide as high, evenly rounded except for the long sloping umbilical wall. There are six to nine irregularly spaced wide constrictions to a whorl, well marked on the internal mould, broadly curved on the sides and crossing the venter with a sharp angle on earlier, more transversely on later whorls. The rib

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Plate 6 ×1 (Fig. 4 ×0·4)

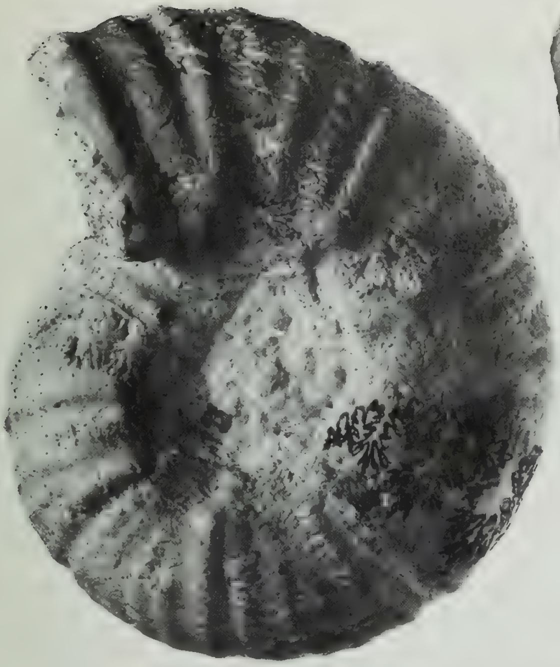
Tongoboryoceras rhodanicum (Roman & Mazeran) (above). Kensworth.
Fig. 1a, b. Specimen with beginning of body chamber, coll. P. R. Payne & R. J. Hogg. IGS Zr 9330.
Fig. 7a, b. Inner whorls, coll. M. J. Oates. GSM 115258.

Pseudojacobites farmeryi (Crick) (p. 313).
Fig. 2a, b. Blount's Farm Pit, Marlow. Holotype of *Pseudopuzosia marlowensis* (Noble). GSM 25456.
Fig. 3a, b. Hitch Wood. Coll. C. J. Wood. GSM 108896. See also Pl. 4, fig. 5 and Pl. 5, fig. 1.

Lewesiceras mantelli Wright & Wright (p. 310).
Fig. 4. Kensworth. Specimen with umbilical tubercles unusually strong and numerous on the body chamber, coll. P. R. Payne & R. J. Hogg. IGS Zr 9329, ×0·4. Fig. 5. Oldbury Hill, Wiltshire. Fragment with unusually strong and regular intermediate ribs. BM 88709. See also Pl. 4, figs 1–3.

Lewesiceras woodi sp. nov. (p. 312). Aston Rowant.
Fig. 6a, b. Paratype. BM C20239. See also Pl. 3, fig. 21.

Photographs: Figs 1–4, 7 by IGS; Figs 5, 6 by BM.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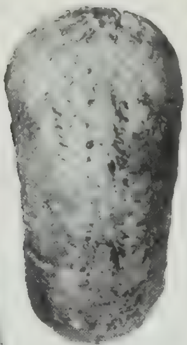
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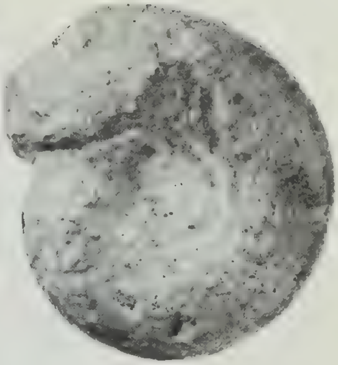
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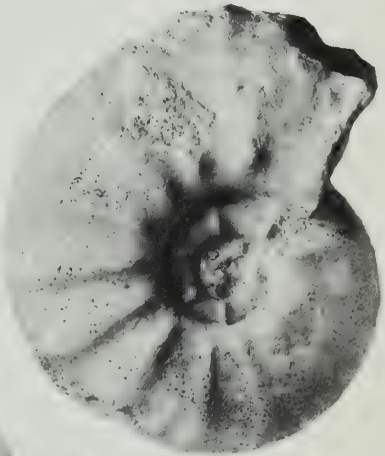
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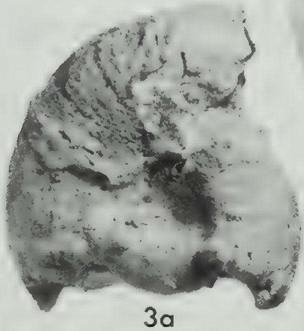
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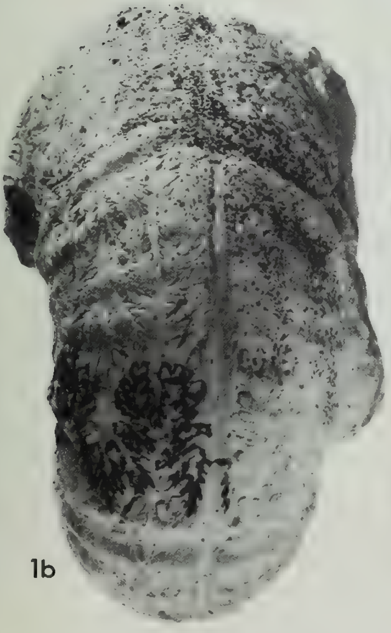
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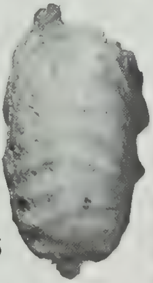
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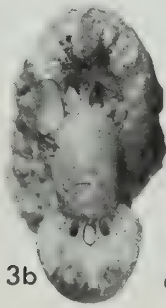
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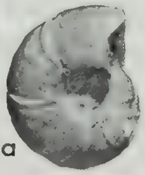
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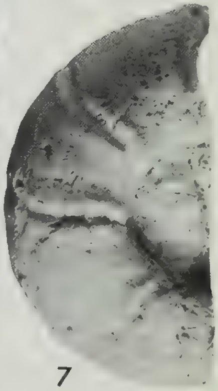
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behind each constriction begins to become stronger from a diameter of about 25 mm, at which intermediate ribs first appear. From a diameter of some 75 mm all ribs are strong, broad and rounded, those on either side of the constrictions united on the umbilical shoulder in a large rounded-bullate tubercle.

Affinities and differences. The inner whorls (e.g. Wainwright coll. J.9 and GSM 115258, *ex* Oates coll.) demonstrate the close relationship with *Pseudojacobites*, but the absence of ventrolateral and siphonal tubercles on the outer whorls and the strong, almost equal ribs distinguish the species and place it in *Tongoboryoceras*. The large Kensworth specimen figured on Pl. 6, fig. 1 (IGS Zr 9330), which agrees well with the holotype, has the beginning of the body chamber preserved at a diameter of 95 mm. The specimen from the Toulmin Smith collection, locality unrecorded (BM 48764), which was figured by Matsumoto (1954 : text–fig. 6) as *Pseudopuzosia marlowensis*, in fact belongs to the present species. It has the prolonged smooth early stage with strong constrictions, angulate on the venter, but the strong intermediate ribs are beginning to appear on the last part preserved.

From the closely related Malagasy Coniacian *T. beantalyense* (Collignon) *T. rhodanicum* differs in having ribs that are slightly curved but not sinuous and much lower and blunter; its constrictions persist to a later stage. *T. tongoboryense* (Collignon) has even more sinuous ribs and a more depressed whorl section. The Turonian *T. donovani* (Collignon) is less depressed than *T. rhodanicum* but is otherwise very similar; the only specimen is too small to show whether the marked feebleness of the ribs persists or not.

Occurrence. Chalk Rock of Kensworth and Blount's Farm pit, Marlow (IGS JM 1354) and chalk immediately above the Chalk Rock at Hitch Wood (IGS Zr 7975); Upper Turonian of Uchaux, France.

Family **COLLIGNONICERATIDAE** Wright & Wright, 1951

Genus ***SUBPRIONOCYCLUS*** Shimizu, 1932

[*Oregoniceras* Anderson, (1941 *nom. nud.*) 1958; *Ledoceras* Basse de Ménorval, 1962]

Type species. *Prionocyclus hitchinensis* Billinghurst, 1927.

The type species is at one extreme of a group of closely allied forms with rather a wide morphological range. The ornament changes somewhat with growth, so that fragments of individuals of different growth rates may be difficult to identify. However, by admitting a reasonable degree of variation in density and strength of ribs and tubercles, a satisfactory grouping into a small number of species can be made. Matsumoto (1959) has fortunately reduced to order the species from California and Oregon and it is simple to tie these in with the European species.

The genus is of particular phylogenetic, and therefore stratigraphic, interest since it appears to be the source of a number of the more important Coniacian and later ammonite stocks. The evolute and coarsely-ribbed *S. branneri*, for example, probably gave rise directly to *Protexanites* and *Paratexanites*, of the Texanitinae; *S. normalis*, on the other hand, appears to grade into *Reesidites* and hence to lead to *Barroisiceras* (Barroisiceratinae).

Subprionocyclus hitchinensis (Billinghurst)

Pl. 5, figs 7–10, 13

1927 *Prionocyclus hitchinensis* Billinghurst : 516; pl. 16, figs 1, 2.
1932 *Subprionocyclus hitchinensis* (Billinghurst) Shimizu : 2.
1951 *Prionocyclus hitchinensis* Billinghurst; Wright & Wright : 30.
1954 *Subprionocyclus hitchinensis* (Billinghurst); Wright & Matsumoto : 129.

Types. The holotype is BM C32292 from Hitch Wood; paratypes are BM 23156 from the 'Middle Chalk of Kent' and C32293 from Hitch Wood.

DESCRIPTION. Very compressed, the whorl section widest at the umbilical tubercles, the sides flat or slightly convex, subparallel to gently convergent, involute, with steeply rounded to undercut umbilical wall. The ribs are wiry and rounded at first but later tend to be flat, at least on the outer part; they are prorsiradiate and slightly sinuous. In the early stages they are single and more or less equal but later arise in twos and threes from slight umbilical bullae; later still they may be more clearly differentiated into primaries with umbilical bullae and about twice as many branching or intercalated secondaries. The ribs end in more or less distinct ventrolateral thickenings or tubercles; on most specimens there are, at some growth stage, perceptible though feeble inner ventrolateral tubercles, but they are normally absent in the young. The keel on internal moulds is entire at first but later develops weak to strong serrations.

There is some variability in the strength and density of the ribs. Some specimens have rather stronger and more distant ribs with more distinct ventrolateral tubercles; these individuals (e.g. Pl. 5, figs 9, 13) are also rather less involute and have less convergent sides and a flatter venter with a more crenulate keel. Thus they somewhat resemble some specimens of *S. normalis* (Anderson), but their ribs are not as flat or as coarse, at corresponding diameters, as in that species.

The suture has rather narrow, deep and coarsely and irregularly subdivided elements; the first lateral ('external') saddle is marked in some individuals by well-developed 'oblique trifidity' such as characterizes *Diaziceras* and other members of the Barroisiceratinae.

AFFINITIES AND DIFFERENCES. *S. hitchinensis* is readily distinguished from *S. branneri* and *S. neptuni* by its involution and compression, and from *S. normalis* (which it resembles in these features) by its finer and denser ribs, which are also less emphatic and less tuberculate on the shoulders.

OCCURRENCE. *S. hitchinensis* is widespread in the Chalk Rock and the nodular facies of the *Holaster planus* Zone and has even occurred in the normal chalk at this horizon in Devon (BM C79657, WW *ex* Reid coll.).

Subprionocyclus neptuni (Geinitz)

Pl. 5, figs 2, 3

1841 *Ammonites bravaisianus* d'Orbigny : 308; pl. 91, figs 3, 4.
1842 *Ammonites falcatus* Mantell; Geinitz : 67 (*non* Mantell).
1850 *Ammonites Neptuni* Geinitz : 114; pl. 3, fig. 3.
1855 *Ammonites Bravaisianus* d'Orbigny; Sharpe : 52; pl. 23, figs 8, 9.
1872 *Ammonites Neptuni* Geinitz; Schlüter : 36; pl. 11, figs 2, 5, 7, 8, ? 9 only.
1872 *Ammonites Bravaisianus* d'Orbigny; Fritsch : 29; pl. 8, fig. 5; pl. 16, fig. 4.
1872 *Ammonites Neptuni* Geinitz; Fritsch : 30; pl. 3, fig. 4 only (*non* pl. 2, fig. 3 *nec* pl. 14, fig. 3).
1872 *Ammonites Neptuni* Geinitz; Geinitz : 85; pl. 36, fig. 4.
1874 *Ammonites Neptuni* Geinitz; Geinitz : 280; pl. 62, fig. 4.
1875 *Ammonites Neptuni* Geinitz; Geinitz : 185; pl. 36, fig. 4.
1877 *Ammonites Neptuni* Geinitz; Fritsch : 101.
1896 *Prionocyclus Neptuni* (Geinitz) Woods : 77; pl. 2, fig. 11; pl. 3, figs 1, 2 only.
1902 *Schloenbachia knighteni* Anderson : 119; pl. 1, figs 1–4; pl. 2, figs 39, 40.
1902 *Schloenbachia siskiyouensis* Anderson : 119; pl. 1, figs 19, 20.
1913 *Prionotropis bravaisianus* (d'Orbigny) Roman & Mazeran : 22; pl. 1, figs 13–18.
1931 *Prionotropis neptuni* (Geinitz) Collignon : 24; pl. 4, figs 1, 2.
1951 *Prionocyclus neptuni* (Geinitz); Wright & Wright : 30.
1954 *Subprionocyclus neptuni* (Geinitz) Wright & Matsumoto : 129.
1958 *Oregoniceras knighteni* (Anderson); Anderson : 264; pl. 24, fig. 5; pl. 33, figs 1, 3 (? *non* fig. 2).
1958 *Oregoniceras siskiyouense* (Anderson); Anderson : 266; pl. 23, figs 2, 3; pl. 24, figs 1–3.
1958 *Oregoniceras jillsoni* (Anderson); Anderson : 267; pl. 19, fig. 6.
1959 *Subprionocyclus neptuni* (Geinitz); Matsumoto : 112; pl. 29, figs 2, 3; pl. 30, figs 2, 3; text-figs 60–63.

LECTOTYPE. The original of Geinitz' figure (1850 : pl. 3, fig. 3) was designated by Matsumoto (1959 : 112).

DESCRIPTION. Moderately but variably involute, rather compressed, the whorl section higher than wide with the sides, at least in costal section, almost parallel for the inner two-thirds or three-quarters, then converging slightly towards the flat to slightly fastigiate venter with its distinct keel. The earliest ribs are low and rounded, rising in twos or threes from indistinct umbilical tubercles. Thereafter to a diameter of 16 to 18 mm (the maximum of most Uchaux specimens – see below) they are rather high and narrow, separated by wider interspaces, arising somewhat irregularly at or near the umbilical shoulder singly or in pairs, rarely in threes, from subdued umbilical tubercles or alternately long and short; the specimen shown in Pl. 5, fig. 2a, b has branching ribs on one side and alternately long and short on the other. The ribs are more or less straight but prorsiradiate until a slight inner ventrolateral tubercle at which they bend sharply forward and end in neat outer ventrolateral clavi. The venter is normally smooth. The keel on internal moulds may be apparently entire or weakly to strongly crenulate. The crenulations are well forward of the corresponding ventrolateral clavi. Normally at a diameter of 16 to 18 mm the ribs become more distant and to a variable extent flatter in their outer part; the specimen shown in Pl. 5, fig. 3 (BM C79655) for example retains the characteristic ribbing of the middle stage until the body chamber. The coarse distant ribbing with correspondingly strong tubercles may persist or may be replaced by closer ribs with the inner ventrolateral tubercles weak or absent, the outer ones reduced and the ribs joining the keel in chevrons on the venter.

AFFINITIES AND DIFFERENCES. *S. neptuni* is more involute than *S. branneri* and has more prorsiradiate, closer and wider ribs and weaker tubercles at corresponding diameters. Some individuals with typical *neptuni* inner whorls, however, have a period of growth with ribs and tubercles like those of *branneri*. The coarsely-ribbed adults figured by Matsumoto (1959 : pl. 29, figs 2, 3; pl. 30, figs 2a, b) are somewhat outside the morphological range found so far in the Chalk Rock. *S. hitchinensis* and *S. normalis* are both more involute and compressed than *S. neptuni* and *S. normalis* has flatter and more sinuous ribs at all stages.

A few fragments (Bromley coll. C.151 and GSM 108932 – see Pl. 5, fig. 11a, b) that at first seem very distinct from *S. neptuni* or any other species of the genus are provisionally included here; they are very evolute and have regular single ribs more prorsiradiate, especially in the outer part, than in typical *neptuni* and a rather narrower venter. The specimen from the Unter Pläner of Plauen figured as *neptuni* by Geinitz (1875 : pl. 62, fig. 4) and included by Woods in the synonymy of this species appears to be a *Watinoceras* from the basal Turonian.

NOMENCLATURE. Examination of specimens showing early and middle growth stages demonstrates that *S. bravaisianus* and *S. neptuni* cannot be maintained as separate species. In their paper on the Uchaux fauna, Roman & Mazeran (1913) refigured d'Orbigny's types and their photographs leave little doubt about the synonymy of the two species. In fact none of the presumed syntypes is large enough to provide an adequate diagnosis for a species in this genus; their range of variation is greater than the difference between the lectotypes of *bravaisianus* (Matsumoto & Noda 1966 : 359) and *neptuni*. The prior name is *bravaisianus* but apart from Moreman's (1927 : 96) description of a specimen as *Gauthiericeras* aff. *bravaisi* (d'Orbigny), passing references by Collignon (1931 : 26) and Basse de Ménorval (1959 : 16, 18) and Matsumoto & Noda's paper (1966) the name has been seldom used since 1913, whereas *neptuni* is regularly and widely used. An application will be made to the International Commission on Zoological Nomenclature to conserve the well-known name *neptuni*.

OCCURRENCE. *S. neptuni* is fairly common and widespread in the Chalk Rock and the nodular facies of the *Holaster planus* Zone. It is widely distributed in north and central Europe and occurs also in southern France, north Africa, Madagascar, California and Oregon.

Subprionocyclus branneri (Anderson)

Pl. 5, figs 4–6

1872 *Ammonites Neptuni* Geinitz; Schlüter : 36; pl. 11, fig. 1 only.
1896 *Prionocyclus Neptuni* (Geinitz) Woods : 77; pl. 3, fig. 3 only.

1902 *Prionotropis branneri* Anderson : 125; pl. 1, figs 11–16.
1927 *Prionotropis cristatus* Billinghurst : 515; pl. 16, fig. 3a–c.
1951 *Collignoniceras cristatum* (Billinghurst) Wright & Wright : 30.
1954 *Subprionocyclus cristatus* (Billinghurst) Wright & Matsumoto : 129.
1958 *Prionotropis branneri* Anderson; Anderson : 261; pl. 34, figs 1–3.
1959 *Subprionocyclus branneri* (Anderson) Matsumoto : 109, text-figs 58, 59.

DESCRIPTION. Rather evolute, whorl section more or less rectangular to square, with sharp, high, coarsely crenulate keel. The ribs are typically almost rectiradiate, simple, high and sharply rounded on the inner whorls but increasingly flattened on the outer; they arise near the umbilical seam, form a pinched bulla on the umbilical shoulder and have two regular and prominent ventrolateral clavi; the corresponding siphonal serration on the keel is well forward of the ventrolateral tubercle. In some individuals, however, a few or even a majority of the ribs spring in pairs from umbilical tubercles. Both types of individuals occur together in the English Chalk Rock and it seems doubtful whether subspecific separation, as provisionally suggested by Matsumoto (1958 : 111), is necessary. Some specimens, moreover, have slightly curved and prorsiradiate ribs (e.g. Wainwright coll. J.15). The suture is as might be expected distinctly simpler, with fewer and shallower indentations than in the more involute and compressed members of the genus.

AFFINITIES AND DIFFERENCES. The squarer whorl section and the more nearly rectiradiate distant ribbing with distinct inner and outer ventrolateral tubercles throughout readily distinguish this species from *S. neptuni*. The other species are all much more involute and compressed.

S. branneri foreshadows *Protexanites* in its ribbing and tuberculation but is at once distinguished by the siphonal tubercles being well forward of and higher than the corresponding outer ventrolateral tubercles. At least one specimen of *S. branneri* (Pl. 5, fig. 6a, b) has incipient midlateral tubercles such as appear in many Texanitinae.

OCCURRENCE. *S. branneri* seems to be rather rare in the Chalk Rock except at Hitch Wood and Kensworth. It occurs sparsely in Germany and Oregon and possibly at Uchaux.

Subprionocyclus normalis (Anderson)

Pl. 5, fig 12a, b; Pl. 7, fig. 2

1872 *Ammonites Neptuni* Geinitz; Schlüter : 36; pl. 11, figs 3, 4 only.
1872 *Ammonites* cf. *goupilianus* d'Orbigny; Schlüter : 37; pl. 11, fig. 10.
1958 *Oregoniceras normale* Anderson : 268; pl. 25, fig. 8, 8a.
1959 *Subprionocyclus normale* (Anderson) Matsumoto : 118; pl. 29, fig. 1; pl. 31, figs 1–5; text-figs 64–66.
? 1962 *Ledoceras massoni* Basse de Ménorval : 871; pl. 22, figs 1–8; pl. 23, fig. 2a; pl. 24, figs 1–5.

DESCRIPTION. Compressed, moderately to very involute and high-whorled with steep to vertical or even undercut umbilical wall and very slightly convex sides. The whorl section is widest just below mid-flank. The venter is flat to fastigiate. The ribs, rising singly or in pairs from slight umbilical tubercles or intercalated, are slightly sinuous to falcoid and prorsiradiate, bending forward more sharply at faint inner ventrolateral clavi, which are absent in early and late growth stages, and ending at moderately strong outer ventrolateral clavi. On the body chamber the inner ventrolateral tubercle disappears, the outer one and the ribs become weaker and the venter more fastigiate, so that there is great similarity to *Reesidites subtuberculatus* (Gerhardt), *R. minimus* Hayasaka & Fukada and certain *Barroisiceras*. The number of umbilical tubercles and ribs varies widely in the American material and the few English specimens fall at the more densicostate end of the range of variation.

AFFINITIES AND DIFFERENCES. *S. normalis* can be considered a compressed and involute version of *S. neptuni* or a flat and sparsely-ribbed version of *S. hitchinensis*. The Californian population is variable; according to Matsumoto (1959 : 120–1) the ratio of umbilical to total diameter ranges from 15% to 30%, the number of umbilical bullae from 7 to 14 and of ribs from 22 to 35. A

Chalk Rock specimen in A. Wainwright's collection (J.15) has, at a diameter of 40 mm, an umbilicus 22·5% of the total diameter, 15 umbilical bullae and 30 ribs. Some of the characters overlap those of *S. neptuni*, but *normalis* differs in being more compressed and involute, with a narrower umbilicus, more fastigiate venter, weaker ornament, sinuous ribs and a shorter stage in which both inner and outer ventrolateral tubercles are present. Californian specimens apparently have only a steeply sloping umbilical wall, whereas the English specimens have it vertical or undercut. As Matsumoto (1959 : 121) points out the resemblance to *Reesidites* is so close that *S. normalis* may be regarded as phylogenetically intermediate between *S. neptuni* and *Reesidites minimus*. Only the brief appearance of lower ventrolateral tubercles indicates the place of *normalis* in *Subprionocyclus*. Basse de Ménorval's *Ledoceras massoni*, whose holotype is a young Uchaux individual figured at twice natural size, includes specimens with slightly more ribs than the most densely costate Californian specimens figured by Matsumoto (1959), but other features are so similar that even subspecific separation seems unnecessary. The Uchaux and English specimens probably occur at a slightly earlier horizon than the Californian ones and the median point of variation in the populations has probably shifted.

OCCURRENCE. Rare at Hitch Wood and Kensworth. It occurs also in the *Holaster planus* Chalk of Surrey and in France and Germany.

General results and correlations

The fauna of the Chalk Rock, occupying at most a part of the lower half of the *Holaster planus* Zone, is, with its relatively numerous species of ammonites, of considerable importance for

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Plate 7 ×1 (Fig. 1 ×3, Fig. 12a ×1·7, Fig. 12b ×1·6)

Scaphites pseudoaequalis Yabe (p. 305). Kensworth.
Fig. 1a, b. Coll. M. J. Oates. GSM 115259, ×3. See also Pl. 3, fig. 5.

Subprionocyclus normalis (Anderson) (p. 321). Kensworth.
Fig. 2. Coll. P. R. Payne & R. J. Hogg. IGS Zr 9331. See also Pl. 5, fig. 12.

Puzosia curvatisulcata Chatwin & Withers (p. 308). Kensworth.
Fig. 3a, b. Coll. P. R. Payne & R. J. Hogg. IGS Zr 7785. See also Pl. 4, fig. 4.

Hyphantoceras reussianum (d'Orbigny) (p. 297).
Fig. 4a, b. Kensworth. Coll. P. R. Payne & R. J. Hogg. IGS Zr 8010. Fig. 6, 1¼ml (2 km) SW of Dunstable. Closely coiled specimen cited by Woods (1896 : 75). GSM 36955. See also Pl. 2, figs 6–7.

Didymoceras saxonicum (Schlüter) (p. 296). Kensworth.
Fig. 5. Specimen showing the earliest regular whorl, coll. P. R. Payne & R. J. Hogg. IGS Zr 7828. See also Pl. 2, figs 8–12.

Scaphites geinitzii laevior subsp. nov. (p. 302). Kensworth.
Fig. 7a, b. Coll. P. R. Payne & R. J. Hogg. IGS Zr 7788. See also Pl. 3, figs 8–9.

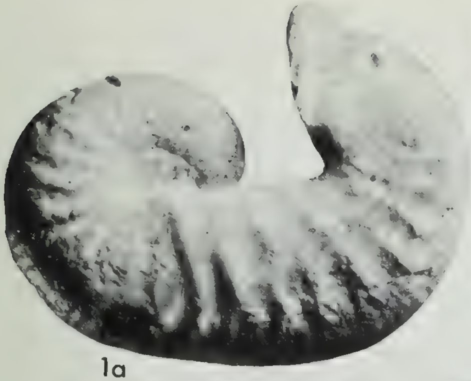
Otoscaphites reidi sp. nov. (p. 307). High Wycombe.
Fig. 8. Pit behind Broom & Wade factory. **Holotype**, coll. C. J. Wood. IGS Zr 7952. See also Pl. 3, figs 17–18.

Scaphites geinitzii geinitzii d'Orbigny (p. 300). Kensworth.
Fig. 9. Specimen with subdued ornament, coll. P. R. Payne & R. J. Hogg. IGS Zr 7786. See also Pl. 3, figs 1–4, 6–7.

Sciponoceras bohemicum (Fritsch) (p. 285). Kensworth.
Figs 10a, b. Coll. P. R. Payne & R. J. Hogg. IGS Zr 7804. Figs 12a, b. Coll. M. J. Oates. GSM 115260. Fig. 12a, ×1·7. Fig. 12b, ×1·6. See also Pl. 1, figs 3–5.

Baculites undulatus d'Orbigny (p. 287). Kensworth.
Fig. 11a, b. Coll. P. R. Payne & R. J. Hogg. IGS Zr 7803. See also Pl. 1, figs 6–8.

Photographs by IGS, except Figs 2, 4a, b, 5, 6, 7a and 8 by BM.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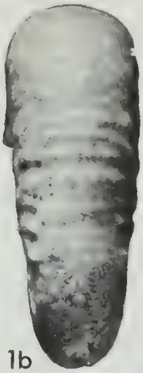
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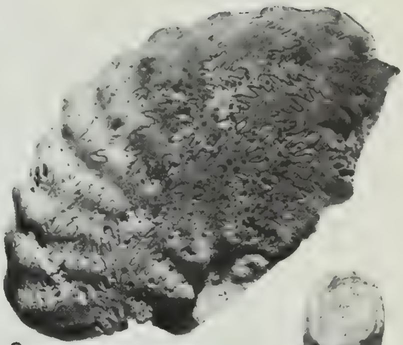
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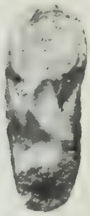
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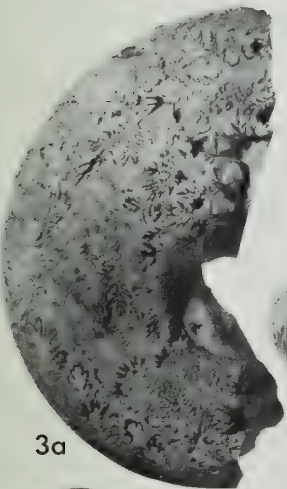
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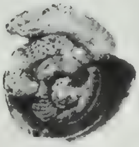
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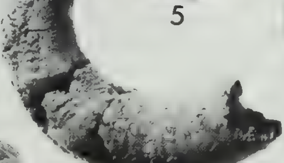
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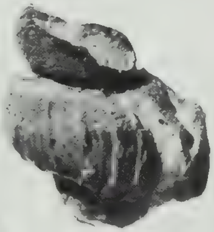
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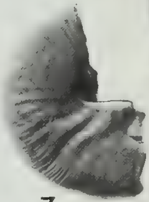
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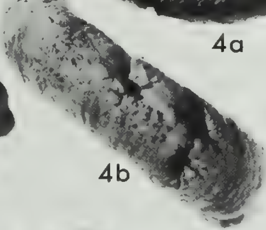
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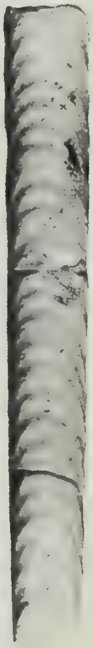
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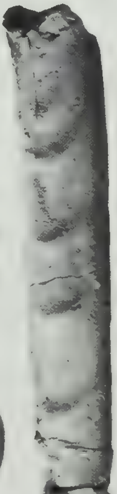
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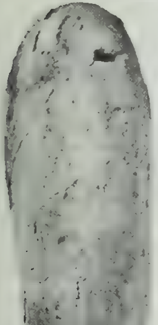
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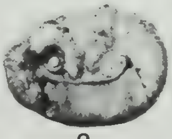
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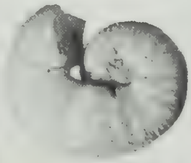
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correlation. As described above, it includes a number of abundant and well-known species as well as various less well known ones and a few genuinely new forms, as listed in the Contents, p. 281.

It is particularly interesting that in various different stocks the beginnings of important evolutionary radiation can be seen at this horizon. For example, *Baculites undulatus*, probably the earliest species of its genus, clearly foreshadows a whole range of Coniacian and later species. The *Scaphites geinitzii* group contains among its many variants the predecessors of a number of Coniacian species. *Lewesiceras* itself is of somewhat restricted morphological range but with *Tongoboryoceras* and *Pseudojacobites*, its presumed derivatives, can be seen as the source of several later genera. *Subprionocyclus* includes *S. branneri* that clearly leads to *Protexanites* and the whole of the Texanitinae, and *S. normalis* that leads to *Reesidites* and thence to the Barroisiceratinae.

There are several European faunas with which that of the Chalk Rock should be compared. The most important is that of Uchaux in south-eastern France, since there also occur there a number of species characteristic of the widespread Tethyan faunas. Unfortunately little is known of the exact horizon of the various ammonite species. Roman & Mazeran (1913) figured 18 species from Uchaux, of which eight, on the basis of the revised determinations given below, also occur in the Chalk Rock. In addition, Basse de Ménorval's (1962) *Ledoceras massoni* from Uchaux is probably a synonym of *Subprionocyclus normalis* and Sornay's (1964) *Lewesiceras romani* is a synonym of *L. mantelli.*

Roman & Mazeran, 1913	Revised determinations
Macroscaphites rochatianus d'Orbigny	*Worthoceras rochatianum* (d'Orbigny)
Hamites gracilis d'Orbigny	*Scalarites* (?) *gracilis* (d'Orbigny)
Hamites sp.	*Hyphantoceras reussianum* d'Orbigny
Baculites undulatus d'Orbigny	*Baculites undulatus* d'Orbigny
Turrilites cf. *costatus* Lamarck	*Turrilites* cf. *costatus* Lamarck
Scaphites aequalis Sowerby mut. *turonensis* nov. mut.	*Scaphites equalis turonensis* Roman & Mazeran
Pachydiscus peramplus Mantell (Sowerby)	*Lewesiceras mantelli* Wright & Wright and *Lewesiceras* sp. indet.
Pachydiscus vaju Stoliczka	*Lewesiceras mantelli* Wright & Wright
Pachydiscus rhodanicus sp. nov.	*Tongoboryoceras rhodanicum* (Roman & Mazeran)
Puzosia gaudemarisi sp. nov.	*Puzosia curvatisulcata* Chatwin & Withers
Puzosia sp.	indet.
Prionotropis bravaisianus	*Subprionocyclus neptuni* (Geinitz)
Prionotropis sp. (pl. 1, figs 18, 19)	*Subprionocyclus* cf. *normalis* (Anderson)
Prionotropis sp. (pl. 4, fig. 18)	*Subprionocyclus* cf. *branneri* (Anderson)
Acanthoceras deverianum d'Orbigny	*Romaniceras deverianum* (d'Orbigny)
Leoniceras groupe de *segne* Solger	*Choffaticeras* (*Choffaticeras*) sp.
Coilopoceras requienianum (d'Orbigny)	*Coilopoceras requienianum* (d'Orbigny)

Despite the two apparent Cenomanian survivors (*Turrilites* cf. *costatus* and *Scaphites equalis turonensis*) the *Lewesiceras*, *Tongoboryoceras* and *Subprionocyclus* common to the faunas of Uchaux and the English Chalk Rock indicate a close approximation of date.

The German Scaphiten Pläner has produced specimens of most of the species recorded from the Chalk Rock, but published stratigraphical information is inadequate to determine whether they all come from a restricted horizon or not. Schlüter (1876 : 222) lists from various localities the following species, given here with revised determinations.

Schlüter, 1876	Revised determinations
Ammonites peramplus Mant.	*Lewesiceras mantelli* Wright & Wright
Ammonites neptuni Gein.	*Subprionocyclus neptuni* (Geinitz) *Subprionocyclus branneri* (Anderson)
Ammonites cf. *Goupilianus* d'Orb.	*Subprionocyclus normalis* (Anderson)
Ammonites Germari Reuss	*Germariceras germari* (Reuss)

Ammonites Bladenensis Schlüt.	*Otoscaphites bladenensis* (Schlüter)
Scaphites Geinitzi d'Orb.	*Scaphites geinitzii geinitzii* d'Orbigny *Scaphites geinitzii laevior* subsp. nov. *Scaphites geinitzii* aff. *intermedius* Scupin
Scaphites auritus Schlüt.	*Otoscaphites auritus* (Schlüter) *Otoscaphites bladenensis* (Schlüter) *Otoscaphites fritschi* (Grossouvre)
Crioceras ellipticum Mant.	*Allocrioceras angustum* (J. de C. Sowerby) *Allocrioceras strangulatum* sp. nov.
Heliococeras spiniger Schlüt.	?
Helicoceras conradi Mort.	?
Heteroceras reussianum d'Orb.	*Hyphantoceras reussianum* (d'Orbigny)
Turrilites saxonicus Schlüt.	*Didymoceras saxonicum* (Schlüter)
Baculites cf. *Bohemicus* Fr. & Schlönb.	*Sciponoceras bohemicum* (Fritsch)

Schlüter also figured from this horizon:

Scaphites sp. ?	*Scaphites lamberti doylei* subsp. nov. or *Scaphites meslei* Grossouvre, subsp. nov.

The Czechoslovakian Teplitzer beds seem to be somewhat later than the Chalk Rock but precise correlation is impossible on the basis of the literature that I have seen. Fritsch (1899) figures or records the following.

Fritsch, 1889	Revised determinations
Ammonites (*Schloenbachia*) *subtricarinatus* d'Orb.	*Peroniceras subtricarinatum* (d'Orbigny)
Ammonites peramplus Mant.	*Lewesiceras mantelli* Wright & Wright *Lewesiceras* sp.
Ammonites (*Desmoceras*) *Austeni* Sharpe	? *Gaudryceras* sp.
Scaphites Geinitzii d'Orb.	*Scaphites geinitzii* d'Orbigny
Helicoceras Reussianum d'Orb.	*Hyphantoceras reussianum* (d'Orbigny)
Helicoceras polyplocum Rom.	*Didymoceras saxonicum* (Schlüter)
Baculites undulatus d'Orb.	*Baculites undulatus* d'Orbigny

From California Matsumoto (1959) recorded *Subprionocyclus neptuni* and *S. normalis* from the Upper Turonian, and said that the former occurred earlier than the latter. Unfortunately, however, a stratigraphically collected series of specimens of *Subprionocyclus* has not yet been described, although California seems to be the most promising area for such a project. These two species occur also in Japan but not enough material seems to be available yet for any refined correlation within the Zone of *Inoceramus teshioensis* (Matsumoto 1971 : 155).

Such evidence as there is points to fairly long ranges for important species such as *Scaphites geinitzii*, *Didymoceras saxonicum*, *Hyphantoceras reussianum*, *Lewesiceras mantelli*, *Subprionocyclus neptuni* and *S. normalis*. Even within the Chalk Rock fauna itself the extent of morphological variation of these species is considerable. Over the whole duration (biochron) of each of these species the mean of the morphological range presumably varied with time, but we are very far from knowing enough of any one population or of the succession of populations in the Upper Turonian to be certain of detailed correlation or to be able to establish refined zonal schemes valid over a wide area.

It is for example possible that evidence will eventually be secured for a zone of *Subprionocyclus normalis* above one of *S. neptuni* or of a subzone of *normalis* within a broad *neptuni* zone. However, even in California and Japan the published evidence does not yet support such an arrangement. What is certain, from the Chalk Rock fauna, is that specimens attributable to *S. normalis* occur with varying forms of *S. neptuni*, *S. branneri* and *S. hitchinensis*. The lesson is that multiplication of zonal or subzonal names based on limited evidence is to be avoided.

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All specimens from the C. W. and E. V. Wright collection (including Mr R. E. H. Reid's ammonites) figured or described here are now in the British Museum (Natural History). The Chalk Rock collection of Mr P. R. Payne and Mr R. J. Hogg and certain of Mr M. J. Oates' ammonites are now in the Institute of Geological Sciences.

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